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ON STENOCHLAENA, LOMARIOPSIS AND TERATOPHYLLUM IN THE MALAYAN REGION.

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Throughout the 19th century the ferns variously ascribed to the above genera were a puzzle to systematists; material was inadequate, and no critical study was made by anyone who had access to the plants in the field. The similarity of adult form in the three groups and the extraordinary degree of polymorphism of juvenile stages of some species led to confusion. An exaggerated idea of possible polymorphism within a species became prevalent, and many quite distinct species were lumped together. Underwood in 1906 was the first author who made a satisfactory arrangement of the species; but he also, through lack of material and of first hand acquaintance with living plants, did not do justice to Teratophyllum. In the past few years I have been able to make frequent observations on the species of Teratophyllum occurring in the Malay Peninsula, and believe that the present account of these is fairly complete. I have also made anatomical observations on these plants, and on species of Stenochlaena and Lomariopsis. Through the courtesy of the Directors of the Botanic Gardens, Buitenzorg and the Bureau of Science, Manila, and of Dr. E. B. Copeland, I have been able to examine the specimens of these genera from the herbaria of Buitenzorg, Manila, and the University of California and from Dr. Copeland's own herbarium; I am greatly indebted for the loan of this valuable material, which has enabled me to give a fairly full account of the species throughout the Malayan region. Further material of many species is however greatly to be desired especially from Borneo and New Guinea. To the Keeper of the Herbarium at Kew I am indebted for photographs of specimens in the Kew Herbarium, and information concerning other specimens. To Dr. van Leeuwen I am indebted for a copy of Raciborski's original description of *Acrostichum Smithii*; to Dr. C. Christensen for advice and information; and to Dr. G. A. C. Herklots for collections of *Teratophyllum aculeatum* and *Asplenium epiphyticum* from Los Banos.

A NOTE ON TERMINOLOGY.

A special term is needed to denote the juvenile leaves of the species of Teratophyllum. Karsten (1895) examined these leaves anatomically and concluded that they served to absorb water; he proposed the name "water leaves," which was also adopted by Christ and other authors. This term is however more appropriate to the submerged leaves of water plants. Further, it is still very uncertain to what extent the juvenile leaves of Teratophyllum perform the function of water absorbtion, and in my opinion a term which does not refer to function, or to morphology, is to be preferred. The characteristic feature of these leaves is that they are produced always and only in the lowest stratum of the forest, near the ground; they are not only borne by young plants, but also by stout branches which start near the ground from old plants. I suggest for such leaves the term *bathyphyll.* The term could be equally applied to the leaves of young aroids, climbing species of Ficus, and other climbing plants which bear specialised leaves in the lower levels of the forest. Other climbing ferns besides Teratophyllum also bear bathyphylls, notably some species of Asplenium (e.g. *A. multilineatum* Brack. and *A. epiphyticum* Copel.) and Lindsaya (*L. repens* (Bory) Bedd.).

HISTORICAL SUMMARY.

The genus Stenochlaena as construed in Christensen's *Index Filicum* is sharply divisible into three groups, as indicated in Underwood's paper. These three groups I here rank as distinct genera: Stenochlaena (consisting of the two subgenera Eu-Stenochlaena and Cafraria, the latter confined to Africa), Lomariopsis, and Teratophyllum. Stenochlaena proper has no specialised bathyphylls; its species are sun plants, contrasting with the species of the other two genera, which (at least in the Malayan region) are plants of shady forest. It is absent from the New World. Lomariopsis also has no specialised dissected bathyphylls in the Malayan region (though some African species have bathyphylls of a different morphological nature from those of Teratophyllum). Lomariopsis is found throughout the tropics, in both Old and New Worlds. Anatomically it is simple, and its species are all very closely allied. Teratophyllum is found only in the Malayan region. It is characterised especially by the production of bathyphylls which are quite different in form from the adult leaves. The three genera have been much confused in botanical literature. The following is a historical summary of their treatment.

Stenochlaena. The common and widely distributed species of Eu-Stenochlaena, *S. palustris*, was first described as *Polypodium palustris* by Burmann in 1768. It was subsequently renamed *Onoclea scandens* by Swartz, and under one or other of these two trivial names was referred by various authors to six other genera. In 1841 John Smith founded the genus Stenochlaena, citing as the first species " *Acrostichum scandens* Linn.", an error in citation; but his intention is quite clear, and *S. palustris* is regarded as the type species of the genus. In his paper on the genera of ferns, published the same year, Smith made the mistake of ascribing to *S. palustris* some bathyphylls of *Teratophyllum aculeatum;* apparently the two were collected together by Cuming. This error was copied by Hooker (*Spec. Fil.* 5, 250), it is found again in the *Synopsis Filicum,* was accepted by Diels, and finally even Copeland (1929, p. 75) appears to share the same opinion, though he says that " other Philippine species are more conspicuous than *S. palustris,* by the production of a series of compound juvenile forms." Other authors did not make this mistake. Kuhn in 1869 founded the genus Teratophyllum for the ferns with specialised bathyphylls, and included *S. palustris* in the genus Lomariopsis. Christ also, though he had such exaggerated ideas on the bathyphyll question, did not ascribed any such to *S. palustris,* neither did Raciborski nor Bishop Hose, who knew the plants in the field. No specialised juvenile forms have ever been ascribed to the other two species of Eu-Stenochlaena. *S. laurifolia* Presl has always been regarded as a distinct species. *S. areolaris* was described by Harringtion as a Lomaria, and was recognised as a Stenochlaena by Copeland in 1908.

Lomariopsis. This genus was founded by Fée in 1845. He referred to it not only the species now so designated, but also those now separated in the genus Teratophyllum. Of Malayan Lomariopsis (in the strict sense) he included *L. cochinchinensis* (which had previously been named *Stenochlaena spondicifolia* J. Sm), *L. Smithii* (previously called *S. longifolia* J. Sm.), and *L. leptocarpa.* Hooker, in the *Species Filicum,* vol 5, would not recognise these as distinct, but included all of them in *Acrostichum sorbifolium* Linn., which name was given originally to a Lomariopsis from the West Indies. Hooker also added to the same species some specimens belonging to Teratophyllum. In this he was followed by Baker, Christ, and Diels. Kuhn and Raciborski however had both recognised the distinctness of the Teratophyllum species.

Teratophyllum was founded by Kuhn in 1869, to include all the ferns with specialised bathyphylls; these were all referred to the species *T. aculeatum* (Bl.). Kuhn also included a second species *T. articulatum,* which was included in Polybotrya by later authors and is now referred by Copeland to Lomagramma. In 1828 Blume had listed under the heading "Lomariae dubiae" *L. aculeata* and *L. gracilis,* the two forms of Teratophyllum found in Java, and had considered their bathyphylls to be fertile leaves. The next species to receive a name was *Stenochlaena limonifolia* J. Sm., founded on a specimen of Wallich's from Singapore; this was later renamed *Lomariopsis ludens* by Fee. It has such polymorphic bathyphylls and has been so inadequately collected that it has never been properly understood, and is described completely in the present paper for the first time. In Underwood's paper another species is described from the Philippines, *S. Williamsii,* and Christ later added *S. arthropteroides.* From the Malay Peninsula Bonaparte described *S. rotundifoliata,* from a juvenile plant only; this also is here described completely. Two further species, *T. Koordersii* from Celebes and *T. luzonicum* from Luzon are described in the present paper.

The bathyphyll question was one that puzzled all authors. Besides those already quoted, Beddome figured two forms in the Ferns of British India (plates CCIX,CCX), prudently refraining from giving names to them. Karsten in 1805 published a short description, with illustrations, of a Teratophyllum from Amboyna, and some observations on the structure and possible functions of the bathyphylls, which he first called "water-leaves," as he believed that they absorbed water. Bishop Hose from Sarawak sent to Christ specimens of bathyphylls of Teratophyllum; unfortunately he made the mistake of placing some of them with adult specimens of Lomariopsis with the statement that both came from the same plant (apparently neither he nor Christ recognised the difference between the adult fronds of Teratophyllum and Lomariopsis). This only served to confirm Christ's ideas about the polymorphism of these plants. In 1896 he remarked that it was difficult to tell whether bathyphylls should be assigned to *Stenochlaena palustris* or to *Lomaria sorbifolia,* and he used Bishop Hose's authority to refute the validity of Kuhn's genus Teratophyllum. In 1897 appeared the *Farnkräuter der Erde,* in which are lumped together under *Lomariopsis sorbifolia* all ferns referable to Lomariopsis and Teratophyllum, and also *Scolopendrium Durvillaei* Bory, which has bathyphylls of a somewhat similar nature. After that Christ evidently assigned every asplenioid fern with bathyphylls to the genus Stenochlaena. In 1905 he returned to the subject, and gave some further details on the structure of bathyphylls. In 1906 (1) he gave a more extended statement of his opinions, with illustrations. By that time he evidently recognised that ferns bearing specialised bathyphylls should be divided into species or subspecies, and that the differences in bathyphylls might have a systematic significance. He still insisted however on including in the genus Stenochlaena not only species of Triphlebia and Diplora (as then understood) but also *Asplenium multilineatum* Brack. and *A. epiphyticum* Copeland. Though he recognised that a comparable dimorphism of leaves occurred in *Lindsaya repens* (Bory), and also compared the bathyphylls of Stenochlaena to the aphlebiae of fossil ferns, apparently he did not recognise that he might be mixing together two or more quite distinct groups of ferns because they possessed superficially similar bathyphylls. He overlooked the articulation of the pinnae, and the characteristic scaliness, of Teratophyllum bathyphylls (though Hooker had remarked on both these points) and evidently he never made any anatomical comparisons, either of juvenile or mature plants. The general conclusions of Christ's papers are that the species of Stenochlaena (in the broad sense) are acrostichoid derivatives of asplenioid origin; Christ regarded *Asplenium epiphyticum* as an immature state of a Stenochlaena bearing asplenioid sori. In 1907 he dealt with Philippine Stenochlaenas, and again he "does not hesitate" to identify *Asplenium epiphyticum* with *Stenochlaena aculeata* (Bl.) Kze. In his remarks on the genus Stenochlaena he referred to Underwood's paper (which appeared the previous year) remarking that "our knowledge of the last group [Lomariopsis] is not sufficiently complete to determine whether or not the secondary leaves are present or lacking, but I am of opinion that they are present, at least in some species." He had of course no definite evidence of this. In 1913 Copeland referred to this paper of Christ's and remarked that *Asplenium epiphyticum* always remained an Asplenium and never changed into a Stenochlaena.

In 1906 appeared Underwood's paper, in which he correctly divided Stenochlaena (so far as the Malayan region in concerned) into the three sections. Since that time further material has been collected, and the examination of this, together with my own observations on local plants in the field and the laboratory has led me to the conclusion that the three sections should be separated as distinct genera.

It is unfortunate that Bower had evidently little first hand knowledge of the genus. His treatment in *The Ferns*, Vol. 3, is hardly in advance of Christ's *Farnkräuter der Erde*.

van Alderwerelt van Rosenburgh, in his book on Malayan Ferns, and the supplement, follows Underwood, with small changes, and the addition of later described species.

Copeland in his paper on the Oriental genera of Polypodiaceae (p. 75) evidently has doubts as to the homophyletic nature of the genus Stenochlaena. But he supports Christ in the opinion that Stenochlaena (as typified by *S. palustris*) is derived from Asplenium, regarding the affinity as "absolutely clear," and contradicting Bower's opinion that Stenochlaena is of Blechnoid origin.

Key to the genera

1. A narrow row of areolae along each side of the midribs of the pinnae *Stenochlaena*
    fertile pinnae simple §*Eu-Stenochlaena*
    fertile pinnae pinnate §*Cafraria* (Africa).

1. No areolae; veins springing direct from midrib 2.

2. Rhizome slender cylindrical, often spiny, scales small; terminal pinna articulated *Teratophyllum*

2. Rhizome of adult plant stout flattened covered with large scales; terminal pinna not articulated *Lomariopsis*

Citation of specimens.

In the lists of specimens following each species, the herbaria in which specimens occur are indicated in brackets after each citation as follows: Buitenzorg HB, California HCal, Copeland HC, Manila HM, Singapore HS, F.M.S. Museums (now incorporated in the Singapore Herbarium) FMS Mus.

Excluded species.

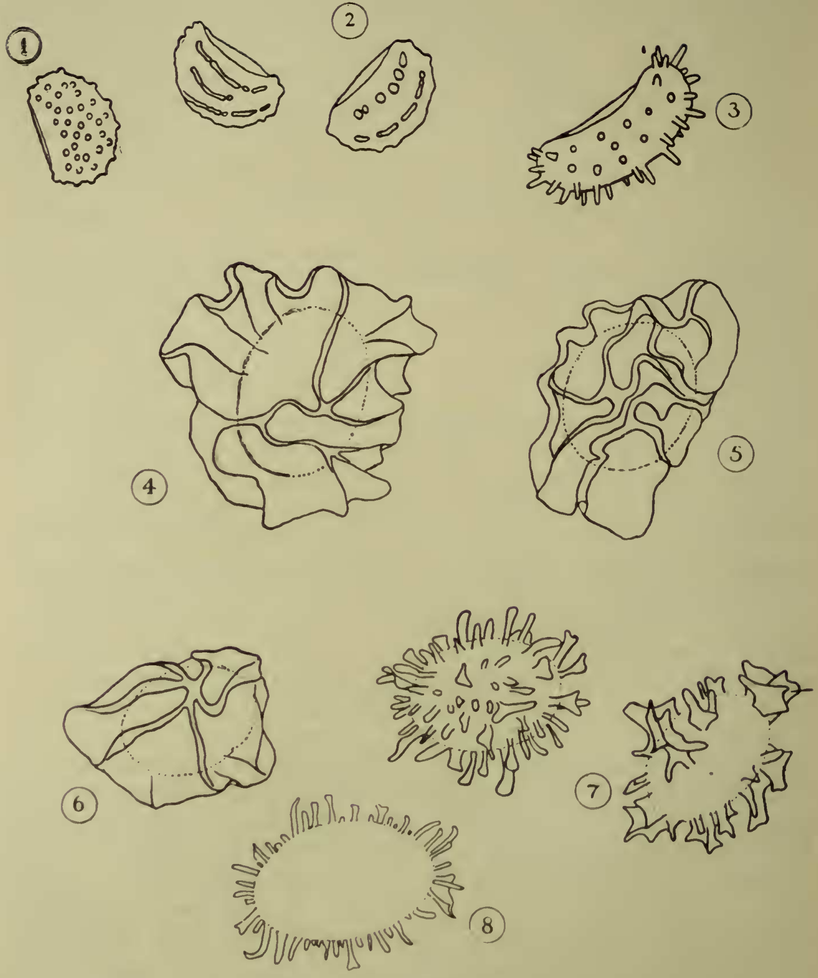
Stenochlaena dubia v.A.v.R. Bull. Dep. Ag. I.N., 1908, XVIII, 26.

This species is based on a sterile specimen, from Amboyna, which I have examined. It is certainly not a Stenochlaena, and probably belongs to the genus Thysanobotrya v.A.v.R. (Cyatheaceae).

STENOCHLAENA J. Sm., Journ. Bot. 3,401; 4,149 (1841).

The original publication of the name Stenochlaena occurs in John Smith's enumeration of the ferns collected by Cuming (1841, 1). It is accompanied by the citation of the two species *Stenochlaena scandens* (with citation of Cuming's no. 133 and the synonym *Acrostichum scandens*, Linn.) and *S. longifolia.* The citation *Acrostichum scandens* was an obvious mistake. There can be no doubt that Smith meant *Lomaria scandens* Willdenow, with the description of which are cited as synonyms *Onoclea scandens* Sw. and *Polypodium palustris* Burm.; the latter is the older name, and the species is now known as *Stenochlaena palustris* (Burm.) Bedd. The fern now known by this name is very common and widely distributed, and I think there can be no doubt that it is correctly referred to Burmann's species. It may be taken as the type species of the genus Stenochlaena. *S. longifolia* was a name only; the same plant was later described by Fée under the name *Lomariopsis Smithii.* It is a Lomariopsis, according to the arrangement adopted in this paper. There are two other Malayan species of the genus Stenochlaena; *S. laurifolia* Presl. and *S. areolaris* (Harr.) Copeland. In addition, there is the African *S. tenuifolia,* which is placed in a separate section, *Cafraria* Presl. The three species of Eu-Stenochlaena form a very natural group and differ very markedly from both Lomariopsis and Teratophyllum in their spores, venation and vascular anatomy. The vascular anatomy is very complex, especially in *S. laurifolia;* nothing like this complexity is to be found in the other plants hitherto included in the genus Stenochlaena. The spores are without perispore, and are ridged or covered with warts or spines; the spores of both Lomariopsis and Teratophyllum have a large perispore (see fig. 1–8). The venation of Stenochlaena is characterised by narrow subcostal areolae from which the lateral veins spring; these areolae are absent in the other genera. The above characters so sharply divide the species of Stenochlaena from the species of Lomariopsis and Teratophyllum, which among themselves have such a close agreement, that I consider a generic distinction essential. As will appear later, I suggest that the genus Stenochlaena has had quite a different origin from the other two genera. The superficial similarity of habit, frond form and acrostichoid sori, has masked the fundamental distinctness of these groups.

Among themselves, the three species of Eu-Stenochlaena show some curious differences. In the first place, *S. palustris* is very widely distributed in tropical Asia,



Spores, all about x 320. 1, *Stenochlaena palustris*. 2, *S. laurifolia*. 3, *S. areolaris*. 4, *Teratophyllum gracile*. 5, *T. ludens*. 6, *Lomariopsis cochinchinensis*. 7, *L. leptocarpa*. 8, *Stenochlaena Warneckei* Hieron., from Amani, E. Africa (Lomariopsis).

Australia and Polynesia; *S. laurifolia* is apparently only known from the Moluccas, the Philippines, New Guinea, and Solomon Islands; *S. areolaris* occurs in the Philippines and New Guinea. *S. laurifolia* is peculiar in that its pinnae are not articulate (the articulation of the pinnae of some specimens of *S. palustris* is incomplete, but the lower pinnae at least are fully articulate), and on this ground it is to be regarded as the most primitive species; its vascular anatomy is also much more complex than that of *S. palustris,* but that may be merely a reflection of its large size. The fertile fronds of the three species also show some differences. The fertile pinnae of *S. palustris* are narrow, and their margins are not recurved. The fertile pinnae of the other two species are broader, and have reflexed margins, much as in the Pteroid ferns, but the veins are continued into these reflexed margins. All three species agree in having a gland (or occasionally two glands) at the base of each pinna, and in the toothed cartilaginous margin to the pinnae, close to which the ends of the veins unite to form a submarginal vein.

I omit reference to Presl's species *S. juglandifolia* and *S. fraxinifolia,* as their identity, from description, is doubtful.

The African fern *Stenochlaena tenuifolia* (Desv.) Presl is clearly very closely allied to these Asiatic species, and should be retained in the genus Stenochlaena. It forms the section *Cafraria* Presl, the other species being placed in the section *Eu-Stenochlaena.* The vascular anatomy and the form and venation of the sterile fronds of *S. tenuifolia* agree exactly with those of the species of *Eu-Stenochlaena;* the rhizome and stipes are very stout, about as in *S. laurifolia.* The pinnae are not articulate, and are relatively long and narrow with parallel sides; they have glands at the base. The fertile pinnae are the distinctive feature, being pinnate instead of simple, with very narrow segments. The pinnules have narrow subcostal areolae, the outer veins of which lie close to the lower surface and bear branches of short tracheid masses only. This simple venation is related to the narrowness of the segments and their thin texture.

A sheet in the California University Herbarium, labelled "Nilgherries, Munro," bears a sterile frond indistinguishable from *S. tenuifolia,* and portions of sterile and fertile fronds typical of *S. palustris.* It may be that the specimens are not all from the same locality; but if they are the sterile specimen may indicate a link between Eu-Stenochlaena and Cafraria.

Key to the species of Stenochlaena.

1. Pinnae not articulated, fertile pinnae 7–10 mm. wide *S. laurifolia*
1. At least the lower pinnae articulated 2
2. Fertile pinnae with reflexed margins; small plant with leaves to about 50 cm. long *S. areolaris*
2. Fertile pinnae without reflexed margins; large plant with leaves to more than 100 cm. long *S. palustris*

1. Stenochlaena palustris (Burm.) Bedd.

This very well known fern needs no detailed description of its external morphology. Some interesting features of its anatomy however seem never to have been published; my investigations on this question are described below, also some observations of a biological nature, and on the variability of the species. For synonymy, see *Index Filicum.*

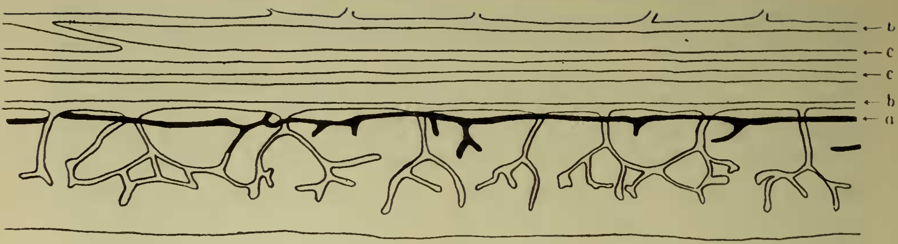
The rhizome of *S. palustris* is smooth. Its apex, and the very young fronds, are covered with imbricating dark brown peltate scales with a narrow thin pale edge, adhering closely; these scales are later deciduous. On actively growing rhizomes of some plants in Pahang I found scales with the thin chaffy edge prolonged towards the apex of the rhizome or frond, and spreading, but there were intermediate types between these and the usual round scales. The leaves are distant, and are borne on all sides of a scandent rhizome. Where a rhizome creeps on the ground, or passes through or over debris in which it can root, it produces roots either on one or on all sides; if it roots on one side, it is somewhat dorsiventral in structure, and leaves are borne only on the side opposite to the roots, but the side of the rhizome on which roots are produced is apparently not fixed as it is in Lomariopsis and Teratophyllum.

The rhizome has a complex vascular structure, as indicated by fig. 9. p. 257. In a transverse section four to six large strands are seen forming an inner ring; round these are smaller strands forming another ring; finally there is a peripheral ring of numerous small bundles. The inner ring of bundles anastomose freely, forming a kind of perforated dictyostele with narrow gaps. Where a leaf occurs, one of the gaps gives off strands to the leaf trace, which also receives supplies from the middle and outer rings of bundles. The bundles of these rings also anastomose together laterally, and the bundles of each ring are supplied from the ring within it. I have not investigated these inter-relations in detail. Each bundle is surrounded by a narrow band of sclerenchyma; the ground tissue is in part lacunar, with peripheral sclerenchyma.

The stipes also are very complex in structure. Fig. 10 shows a transverse section of a large stipe, having more than 40 vascular bundles of various sizes. A smaller stipe had 18 bundles. At first sight the arrangement appears almost a haphazard one, but there is a more or less definite pattern. The rachis has a smaller number of bundles, which is finally reduced to the three central large strands just below the terminal pinna (fig. 16). The stalk of a lateral pinna has four strands (fig. 15), the two lateral ones forming the outer veins of the narrow areolae beside the midrib. Of the two central bundles, the upper (adaxial) one divides again, and thus the three bundles of the midrib of the pinna are produced (fig. 14). In the terminal pinna the structure of the midrib is the same; three bundles enter it from the rachis, and the two lateral ones divide, forming the outer veins of the areolae.

The fertile pinnae have a vascular supply to the midrib and areolae identical with that of the sterile pinnae. The lateral veins however have special branches serving to supply the sporangia; these branches are not all in one plane, and thus the figure by Mettenius republished by Diels (p. 252, fig. 1330) does not give an accurate representation of them. They can only be seen distinctly if a pinna is cleared (in eau de javelle) and the sporangia and also the sclerenchyma overlying the lower side of the midrib are carefully removed. If a pinna so treated is examined with a binocular dissecting microscope the veins are seen in perspective and the different levels at which they lie can be observed. The result is shown in fig. 12, and fig. 13 shows a transverse section. It will be observed that in the thickest part of the pinna, near the midrib, a continuous vein runs close to the lower surface; this soral vein is distinct from the outer vein of the subcostal areolae (which lies nearer to the upper surface of the pinna) and appears to be supplied from the areolar vein. The soral vein has also some lateral branches, all close to the lower surface. The normal lateral veins reach a level close to the lower surface at some distance from the midrib; they then branch, and their branches spread out in superficial tracheid masses, sometimes anastomosing, and supplying the needs of sporangia in the outer part of the pinna, the sporangia nearer the midrib being fed by the soral vein and its branches. This arrangement is similar in character to the diplodesmic vascular systems of other acrostichoid ferns described by Bower.

In many characters *S. palustris* is a very variable species. As regards the size and shape of the pinnae, even within the Malay Peninsula, there is considerable variation. There are specimens the middle pinnae of which are so different in size as 15 by 1.5 cm., 15 by 4.5 cm., 10 by 2.3 cm.,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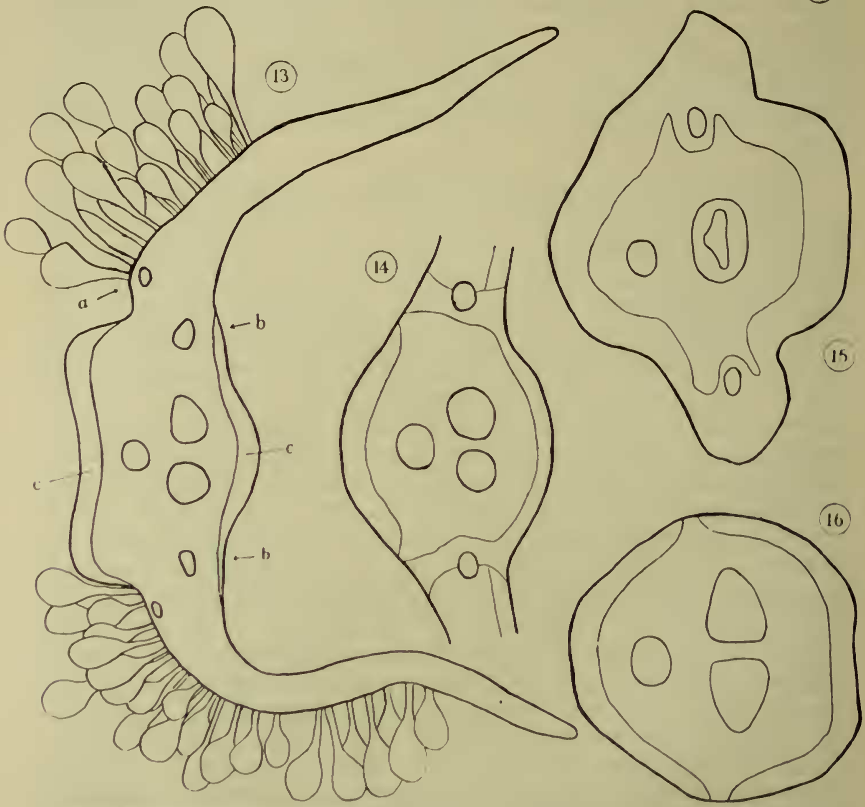
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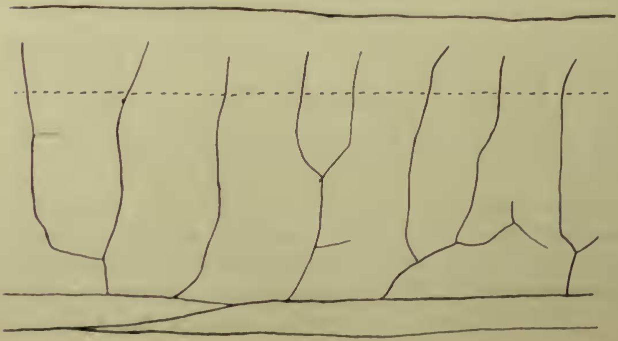
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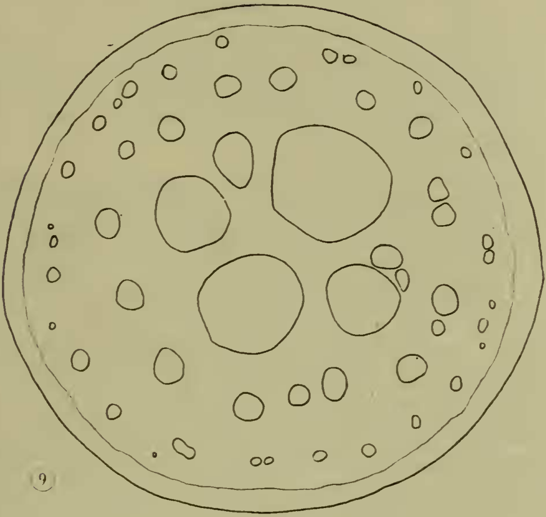
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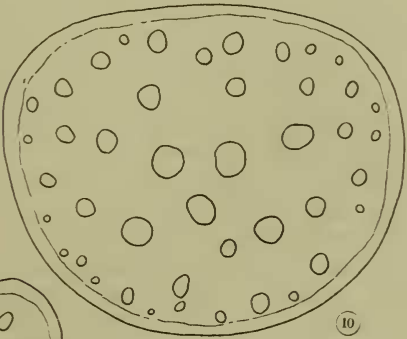
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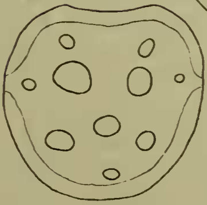


Stenochlaena palustris. 9, t.s. rhizome. 10, t.s. stipe. 11, t.s. upper part of rachis, showing vascular bundles (outline of endodermis) and peripheral sclerenchyma. 9 & 10, x 9; 11, x 14.

12–16, *Stenochlaena palustris.* 12, fertile pinna from below, showing course of vascular bundles; a, soral vein; bb, lateral veins of the subcostal areolae; cc, upper bundles of midrib (lower bundle removed). 13, t.s. fertile pinna; a, soral vein; bb, lateral veins of the subcostal areolae; cc, sclerenchyma. 14, t.s. sterile pinna, showing 3 midrib bundles and the two lateral bundles as in 13. 15, t.s. pinna stalk. 16, t.s. rachis just below the terminal pinna. 17, *S. areolaris*, venation of fertile pinna; the edge of the pinna is folded back along the dotted line. 12 & 17, x 12; 13–16, x 30.

24 by 3.2 cm., 19 by 3.7 cm. The base varies from broadly rounded to rather narrowly cuneate; the sides are sometimes parallel for most of their length, and sometimes the pinnae are widest near their base, gradually tapering to the apex. One specimen from Grik (Upper Perak) has all the pinnae covered beneath with erect simple pale hairs; all other specimens are glabrous.

The articulation of the pinnae is another variable point. One might suppose that pinnae could be described definitely either as articulate or not articulate; but some fronds of *S. palustris* have pinnae which are only partially articulate. In this species fully articulated pinnae have a slight constriction at the base, and this is surrounded by a rather broad, dark, slightly swollen ring on the rachis. This dark ring in section is seen as a broad zone of dark-coloured rather thick-walled cells, passing right across the base of the pinna; it is a very thick absciss layer, quite unlike the thin absciss layer of narrow cells found in Lomariopsis. In many fronds of *S. palustris* the uppermost pinnae have this dark tissue developed only on the side of the pinna-stalk towards the apex of the frond, while on the basal side there is no sign of articulation. In the Malay Peninsula all the fronds I have seen have at least the lower pinnae fully articulate, but in the Philippines and New Guinea even the lowest pinnae are not always properly articulate; one finds in fact almost all gradations between fully articulate pinnae and the complete lack of articulation found in *S. laurifolia*. Thus in diagnosing the distinction between *S. palustris* and *S. laurifolia* other characters than that of articulation need to be considered. One good character is the form of the spores; in *S. palustris* they are irregularly tuberculate, whereas in *S. laurifolia* the tubercles are arranged in definite rows, sometimes almost completely coalescing to form ridges.

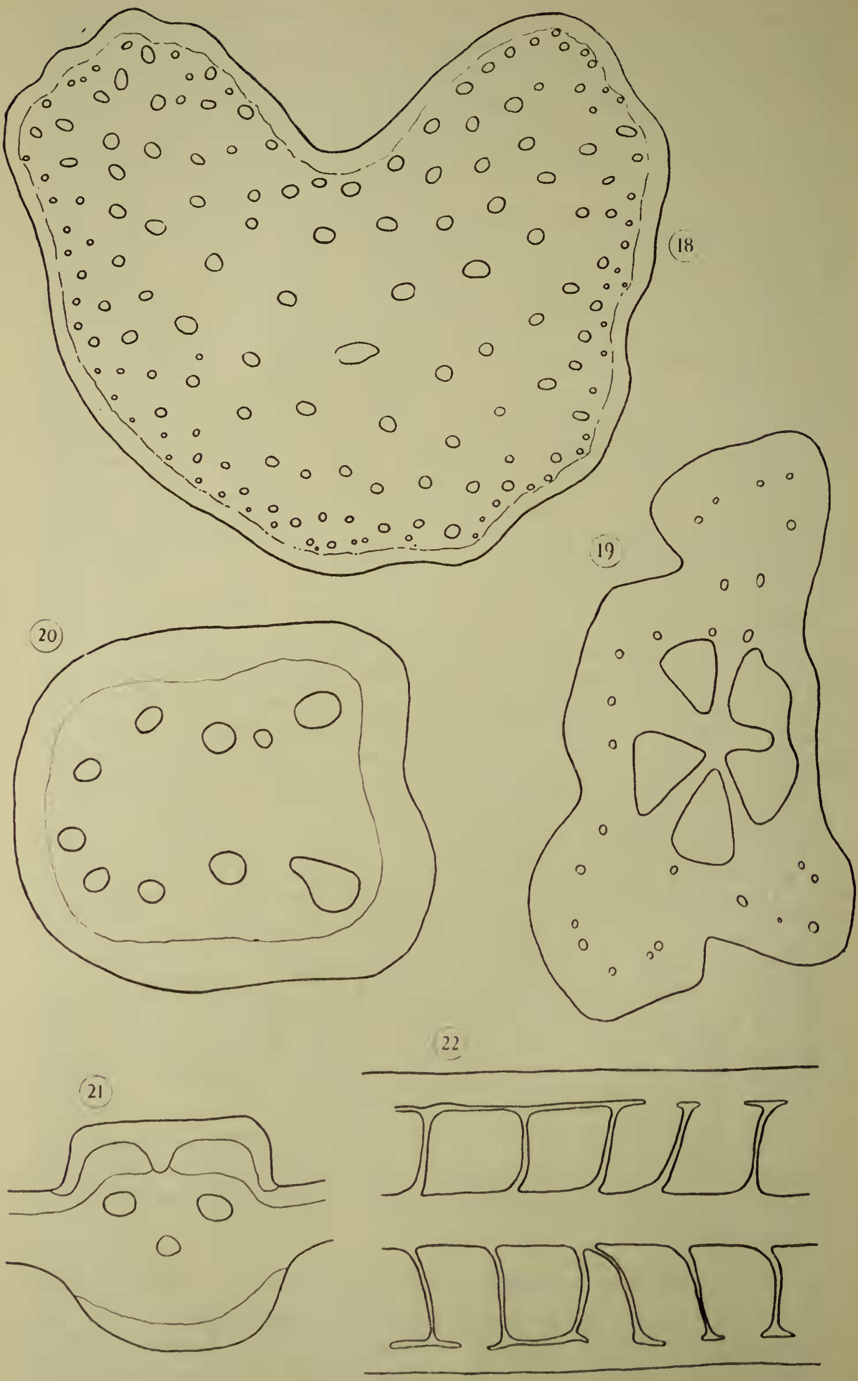
Elmer's no. 18242 from Los Banos, Luzon, is rather intermediate between *S. palustris* and *S. laurifolia*. It has only slight signs of partial articulation at the bases of the pinnae, very large sterile pinnae (24 by 4 cm.), wide fertile pinnae (5 mm. wide) and the spores have rather large tubercles which show some signs of arrangement in rows. Cuming's no. 133 (the specimen in H.C.) has fertile pinnae 5 mm. wide and rather large sterile pinnae broadly rounded at the base and only partially articulated. The spores are irregularly tuberculate. This specimen is from the collection cited by Smith in founding the genus Stenochlaena. Whether or not it is to be regarded as the type of the species *S. palustris* (Burm.) Bedd., it is not really typical of that species over the greater part of the range the species occupies.

S. palustris is a very abundant fern in the Malay Peninsula, in wet places in the lowland country, fully exposed to the sun, or in light shade. Rather open swamp forest in Johore and Singapore is full of this species, a large number of stems climbing up every tree of any size, and scrambling over thickets of vegetation on river banks. As mentioned in a note published by me in 1927, this fern produces fertile fronds at irregular intervals in Singapore, and the production of these fronds is usually found to follow rather unusually dry weather. This is comparable to the production of flowers by evergreen trees as a result of the incidence of dry weather. Though spores of *S. palustris* are thus not infrequently produced, and often in quite large numbers, I have never yet found any sporelings, though I have searched for them in several different localities, and on various occasions, in the neighbourhood of old plants. On one occasion I found what appeared to be a young plant (though it may have been a slender branch of an old rhizome) on the base of a Sago palm. This plant had a very slender rhizome, one simple frond with a stipe 11 cm. long and a lamina 10.5 by 2.1 cm., and trifoliate fronds with terminal pinna 12 by 2.5 cm. and lateral pinnae 5 by 1.6 cm. This is the only simple frond I have seen, and though the plant may not have been a sporeling, it appears to me good evidence that young plants of *S. palustris*, like those of Lomariopsis, first produce simple fronds and then later fronds with lateral pinnae. In the same place I found small trifoliate fronds on slender branches of old rhizomes; some of these fronds were very small, with terminal pinna 5.5 cm. long and lateral pinnae 2.5 cm. long. I have never seen any indication whatever that *S. palustris* has bathyphylls of the same nature as those of Teratophyllum. Indeed, *S. palustris* grows in such open places that no Teratophyllum would tolerate them. It is apparent that *S. palustris* spreads over long distances by its very tough creeping and climbing stems, and stands in little need of propagation by spores. I have recently succeeded in growing its spores on old roots of *Asplenium nidus*. The plants are still very young at the time of writing. The largest leaves are simple, 1.5 x 1 cm. the margin toothed, the veins forming one or two areolae close to the costa.

The species *S. palustris* is widely distributed and well known; I think that no useful purpose would be served by a enumeration of the large number of specimens which I have examined.

2. **Stenochlaena laurifolia** Presl, Epimel. p. 164 (1849).

I have seen neither the type specimen nor the original description of this species. The specimens below enumerated agree well with the descriptions of Hooker (*Spec. Fil.* V, 250) and van Alderwerelt van Rosenburgh (*Malayan Ferns,* 719), except in one point; they all have glands at



18, *Stenochlaena laurifolia*, t.s. petiole 20 cm. from base, showing vascular bundles and peripheral sclerenchyma, x 4. 19–22, *Lomariopsis cochinchinensis*. 19, t.s. rhizome, x 5. 20, t.s. stipe, x 9. 21, t.s. sterile pinna, x 18. 22, venation of fertile pinna, x 6.

the bases of the pinnae, as in *S. palustris*. It is of course possible that the type of *S. laurifolia* is glandless, and in that case the specimens here described may be specifically distinct. But I have observed that occasionally, even in *S. palustris,* some pinnae have no visible gland, and it may be that Presl's specimen also was peculiar in this respect.

Examination of a considerable number of specimens of Stenochlaena from the Philippines and New Guinea reveals the fact that a few of them are rather intermediate in articulation and in width of the fertile pinnæ between *S. palustris* and *S. laurifolia*. Possibly some such specimens are actually hybrids. Evidently the two species are closely similar in habit, and they may grow side by side; of this we have no evidence at present. But the extreme form represented by what appears to be the typical *S. laurifolia* is so different from typical *S. palustris* that the two must be kept specifically distinct. All the specimens below cited agree in the following characters.

The rhizome and stipes are very stout and their vascular anatomy very complex. A small portion of the stipe of Beguin's specimen from Ternate, 20 cm. from the base, when soaked in potash swelled to nearly 2 cm. in diameter; a drawing of a transverse section of this stipe is given (fig. 18), showing the extraordinary number of vascular bundles it contains. The rhizome of the same specimen contains a central ring of 8 large bundles, with smaller peripheral bundles arranged in a similar manner to those of *S. palustris*. The pinnae are all without articulation; the lower ones are almost sessile, very large and stout, the base broadly rounded to subcordate, the edge strongly toothed. The upper pinnae are cuneate at the base. The fertile pinnae are 7 to 10 mm. wide (the largest fertile pinna of *S. palustris* I have seen is 5 mm. wide) ; their edges are distinctly reflexed and sometimes slightly toothed; the veins are continued into the reflexed edge. The venation agrees with that of the fertile pinnae of *S. palustris*, but there is more anastomosis of the veinlets, owing to the additional width of the lamina. The subcostal soral veins are present, with numerous excurrent branches, some of which join other veins; none of the veins reach the edge. The spores (fig. 2) are ridged, the ridges often broken and consisting of rows of tubercles, (as in Bamler's New Guinea specimen).

Dr. van Leeuwen's specimen from New Guinea, gathered at 700 m. altitude, differs from the others in having the pinnae narrower; the sterile pinnae are barely 2.5 cm. wide, and the fertile pinnae at most 6 mm. wide. In complete lack of articulation of the pinnae, and in spore characters, it agrees with the other specimens of *S. laurifolia.* The sterile pinnae are very coriaceous, with prominent veins.

Specimens examined.

PHILIPPINES. Samar, Fagor 1861 (H.C. 6428); sterile. Lucaena, Tayabas, Luzon, Copeland (H.C. 6437); fertile fronds not fully expanded. Lucban, Tayabas, Luzon, Elmer 7736 (H.C., H.B.).

NEW GUINEA. Ins. Rook, Woing, Bamler R. 1 (H. Cal.). Ulaputur, Nieuw-Pommeren, Peekel 35 (HB). Augusta rivier, Gjellerup 345 (HB). Nassau Geb. 700 m., van Leeuwen 10642 (HB).

TERNATE. Sasa-Ketjil, alt. 3 m., V.M.A.Beguin 1170 (H.B., H.M.); distributed from Buitenzorg as *S. palustris.*

CERAM. N. O. van Piroe, W. Ceram, Rutten 1914 (HB). Rant 158 (immature, doubtful, HB).

AMBOYNA. Botter 48 (sterile, HB). Hila, Treub s.n. 1893 (sterile, HB). Soja, Treub s.n. 1893 (young frond, sterile, HB).

3. **Stenochlaena areolaris** (Harr.) Copeland; Philip. Journ. Sci. 2 C, 406 (1908).

Lomaria areolaris Harrington; Journ. Linn. Soc. Bot. 16, 28 (1877). *Original description. Caudex* long, slender, twisted, naked; *stipe* 6 ins. long in the sterile, nearly twice as long in the fertile fronds, glabrous; *barren fronds* ovate, 4–6 inches long, 3–4 inches broad, pinnate; *pinnae* 7–9, lateral nearly sessile, terminal stalked, form linear lanceolate, 2–3 ins. long, ½–¾ in. broad, acute, finely serrate, obtuse or rounded at the base; *texture* coriaceous; *nerves* forming a series of arches close to the midrib, thus forming on each side a row of long narrow areolae parallel to the midrib; beyond this, nerves are free and simple or forking; *surface* naked, except that the midribs and nerves are a little chaffy below; *fertile pinnae* 7–9, narrowly linear, 1½ to 2 ins. long, rather distant; *indusium* narrow, marginal.

Growing among the leaves of a Pandanus, Mount Mahayhay, Luzon; coll. J. B. Steere.

Harrington followed the custom of the time in regarding the industrial characters as all-important, and so referred the plant to the genus Lomaria. He remarked however "were it not for the indusium, which is readily overlooked, except in young plants, the specimens would be placed in the genus Acrostichum, group Stenochlaena."

I have seen a fragment of the type, and several other collections, and add the following notes to the above description. The rhizome is very slender, but still appears to contain a fairly complex vascular system, with an inner ring of about 5 bundles and smaller ones outside. As the whole plant is so much smaller than those of the other two species, a less complex vascular system is to be expected. The mature parts of the rhizome bear no scales, but the very young unexpanded fronds are covered with dark brown scales; these are about 3 mm. long by. 5 mm. wide, have a rounded peltate base from which they are gradually narrowed to an acute apex, and an entire edge. Versteeg's specimen (mentioned by v. A. v. R. in his Supplement, p. 428) has larger fronds than those described by Harrington; they are 25 by 16 cm., with about 7 pairs of pinnae, the largest pinnae measuring 10 by 2.2 cm. Of Dr. van Leeuwen' s collection there are four sheets; three of them show small plants agreeing with Harrington's description, but the fourth has a frond even larger than Versteeg's, the pinnae measuring up to 3.3 cm. wide near the base. The pinnae of all specimens have glands on one or both sides of their broadly rounded to subcordate base. The fertile pinnae on Versteeg's specimen are up to 10 cm. long by 3 mm. broad; those of Dr. van Leewen's to 12 cm. by 6 mm. There is a well marked ridge towards the edge of each fertile pinna, the portion beyond the ridge being turned at right angles to the lamina as in Lomaria; the veins are continuous into this recurved edge but do not reach the margin (fig. 17, p. 256). The costal areolae are present as in the barren pinnae and the remaining veins anastomose slightly, but as far as I have been able to observe there is no specially developed system of veins, as in *S. palustris.* The spores are elongated and spiny (fig. 3). It is interesting to note that three of the four collections were found growing on Pandanus plants.

DISTRIBUTION: Philippines and New Guinea.

Specimens examined:

PHILIPPINES. Mahayhay, Luzon, J. B. Steere (type fragment in HC). Mt. Banahao, Tayabas, Luzon, Elmer 7961 (HC); "quite common but wholly confined to the shaggy branches of *Pandanus utilissimus,* succulent, fragile, 1,600 feet."

NEW GUINEA. Versteeg, 1102. (H.B.). Heuvelterrein, Rouffaer-rivier, 175 m., W. M. Docters van Leeuwen 9909; epiphytic on Pandanus. (H.B.).

LOMARIOPSIS Fée, Hist. Acrost. 66 (1845).

I here divide this genus, as understood by Fée, into Lomariopsis proper and Teratophyllum. These divisions are those adopted as subgenera by Underwood. It is clear that the name Lomariopsis should be retained in the sense employed by Underwood, for the first species described by Fée was *L. cochinchinensis*, and the majority of his species are still retained in the genus, only *L. spinescens* and *L. ludens* being excluded. *L. cochinchinensis* may be taken as the type species of the genus, which may be characterised as follows.

Rhizome climbing, fleshy, broad, rooting below and bearing several rows of leaves above, densely clothed (at least when young) with broad brown scales 1 cm. or more in length, their base narrowly peltate, their margin usually more or less ciliate, their cells brown throughout, not having very thick lateral walls; the vascular structure of the rhizome dorsiventric, showing in transverse section (fig. 19, p. 260) a broadly U-shaped bundle next the lower surface and above this a ring of wedge shaped bundles with narrow leaf gaps between them. Stipe and rachis stout, containing a single row of bundles up to at least 10 in number (fig. 20), scaly like the rhizome when young, later glabrous. Pinnae articulate, except the terminal one which is continuous with the rachis; veins free, usually uniting superficially with the cartilaginous margin, though the vascular bundles do not unite to form a marginal vein; surfaces with scattered minute fimbriate scales of the same character as the rhizome scales. Fertile pinnae usually narrow (sometimes up to 2 cm. wide), their venation simple with no accessory soral veins (fig. 22), the sporangia completely covering the lower surface of the lamina. Spores large, with perispore (fig. 6–8).

Young plants of Malayan species, so far as known, have simple fronds, later and larger fronds bearing articulated lateral pinnae below the terminal pinna. In some African species, apparently, the earlier fronds of young plants may be incised, but bathyphylls like those of Teratophyllum are not found; the segments of the incised fronds are not articulate, and the later fronds are simple and entire, as in the Malayan species of Lomariopsis.

The genus Lomariopsis is distributed throughout the tropics, but I can deal here only with the species found in Malayan region and the Pacific. I have examined a few specimens from Africa and America, and have found in them agreement with the Malayan species in all the points above noted as characteristic of the genus.

The delimitation of the species in this genus is difficult. Hooker's solution was to put them all into one species (with which he also included most species of Teratophyllum). But it is clear that many distinct forms can be recognised which ought to be ranked as separate species. Typical specimens of *L. cochinchinensis* and *L. leptocarpa,* for example, are very different from one another. But one finds other specimens which are rather intermediate between the two, and a good deal of field study, especially in New Guinea, the Moluccas and the Philippines, is needed before satisfactory species groupings can be made. There is a good deal of variation in frond form in the species *L. cochinchinensis*, which I have seen growing in many places; also much difference between fronds of old and young plants. To found a new species on an odd collection, unless that species be strikingly distinct, is unsatisfactory. *L. Raciborskii* and *L. Kingii* are species of this type, which I do not feel are well characterised. I retain the names, because the material at my disposal does not enable me to make any better arrangement; but I regard the present treatment of the species of Lomariopsis as only tentative. The specific distinctions are in some cases so vague that I have found it impossible to make a workable key. A geographic classification is the only possible one at present.

L. cochinchinensis is the most widely spread species in the region under review, extending from Cochinchina in the north throughout the Malayan region to New Guinea (whence quite typical specimens have been obtained). It appears to be normally a lowland species. In the Philippines occurs *L. Smithii,* which should perhaps be reckoned only a variety of *L. cochinchinensis;* but more field study of this is needed. *L. leptocarpa*, on the mountains of Java, is a remarkably uniform species; the type of that species however was from the Philippines, and unfortunately we lack really good specimens from the Philippines for comparison, and the only collection made in the intervening region is from B. N. Borneo. *L. leptocarpa* extends to the mountains of Sumatra, as far north as Brastagi, but is not known in the Malay Peninsula. Further collections may be expected from the mountains of Sumatra and Borneo. *L. subtrifoliata* from the Philippines and *L. oleandrifolia* from Fiji are very closely allied together, and form perhaps the most strikingly distinct group of the genus. It would be very interesting to know how far these two ferns are represented in the islands lying between the Philippines and Fiji, and how far the distinction of the very long stalked pinnae of the Fiji species will hold good; whether there is a gradual change to the long stalked condition as one passes from one territory to the other. From the Moluccas we have *L. Raciborskii,* apparently only known from plants cultivated at Buitenzorg. In New Guinea is the very large *L. intermedia;* also *L. Kingii* (somewhat intermediate between *L. leptocarpa* and *L. cochinchinensis*); there are also some New Guinea specimens which may belong to a further species, but at present I can only regard them as rather extreme forms of *L. cochinchinensis*. In Fiji is a fairly distinct but variable species *L. Brackenridgei*, and in Tahiti and Samoa is *L. Setchellii*, again not a very strongly characterised species, so far as one can judge from two specimens. In New Caledonia is *L. novae-caledoniae*, apparently quite distinct.

1. **Lomariopsis cochinchinensis** Fée, Hist. Acrost., 66, t.26 (1845)

Lomaria ? spondiaefolia Wall. Cat. 37 (Singapore).

Stenochlaena spondicifolia J. Sm. 1841 (nomen).

Stenochlaena abrupta v. A. v. R., Bul. Buitenz. 1915, XX, 24.

Stenochlaena cochinchinensis Und., Bull. Torr. Bot. Cl., 33, 46 (1906).

I have not seen the type of this species, which is from Cochinchina. Typical specimens from the Malay Peninsula agree closely with Fée's figure, and the following description is based on Peninsula plants, of which I have seen a considerable number in the field, in several localities.

Young plants bear simple fronds, progressively larger. The smallest fronds seen are only 2.5 cm. long; the largest simple fronds are about 30 cm. long by 6 cm. wide, on stipes up to 15 cm. long. Except on the very youngest plants, these simple fronds, like the pinnae of pinnate fronds, are abruptly contracted just below the narrow acuminate apex, which is about 2 cm. long. They are narrowed gradually to the base. Two specimens with simple fertile fronds have been seen, the fronds not quite fully acrostichoid. After the largest simple fronds, the young plants bear fronds with one or more pairs of broad sessile lateral pinnae below the terminal one. Often the abrupt contraction of these is very marked.

Adult plants. The rhizome agrees with the general description given for the genus (p. 264). It is very thick and fleshy and is ridged above with decurrent leaf bases. A section is shown in fig. 19. The stipes are up to about 20 cm. long, and the frond to at least 80 cm. long and 30 cm. wide, the pinnae to about 20 pairs. The stipe and rachis are scaly when young; later most of the scales, except the small ones, are lost. The basal or sub-basal pinnae are the largest, being up to 20 cm. long and 5 cm. wide, on stalks 3 to 5 mm. long, their base unequal, narrowly cuneate on the lower and broadly on the uper side, their margins almost parallel over most of their length, suddenly contracted to a caudate apex, the cauda 2 to 3 cm. long, the margins entire cartilaginous, the texture subcoriaceous, surfaces bearing scattered minute brown fimbriate scales, pale beneath and darker above, the midrib prominent below and grooved above when dry, the veins slightly prominent on both surfaces, simple or forked near the base, 1.5 to 2 mm. apart. The apical pinna is continuous with the rachis, on large fronds only 8 to 10 cm. long and 3 cm. broad, but larger on smaller fronds. Fertile fronds bear up to 20 pairs of pinnae which are about 8 to 15 cm. long and 3 to 6 mm. wide, on stalks up to 8 mm. long, their veins simple or forked near the base, uniting sometimes close to the margin, the whole lower surface covered with sporangia.

The above description applies to typical large fronds of adult plants from lowland forest. There is however some variation even among lowland plants. The pinnae have not always the very abrupt contraction near their apex; this applies especially to the upper pinnae of large fronds. In the case of young plants with few pinnae on each frond, the pinnae are usually quite sessile and show the subapical contraction very markedly; *S. abrupta* v.A.v.R was based on such specimens. The larger fronds of older plants have usually stalked pinnae and the subapical contraction less abrupt or even almost absent on the upper pinnae. Sometimes the pinnae of adult plants may be much narrower than normal; *e.g.* my 24946 from swampy forest by the Endau river, Johore, growing close to typical specimens, has pinnae 17 cm. long and only 2.3 cm. wide. Some of the pinnae of this specimen are also gradually narrowed to their apex, though others show the contraction in a moderate degree. This leads on to a specimen from Ginting Sempak (1500 ft. altitude) which has pinnae all gradually tapered to the apex. From Fraser's Hill (3500 ft.) and Penang Hill (probably about 2000 ft.) are specimens with rather small pinnae (only about 12 cm. long) showing only a slight subapical contraction. The differences exhibited by these specimens are quite inadequate to characterise them as distinct species; I therefore include them here. The spores of the Fraser's Hill plant agree with those of typical specimens of *S. cochinchinensis*, differing markedly from spores of *L. leptocarpa* from Java and Sumatra (see fig. 6, 7, p. 252).

There are three specimens, widely scattered geographically but agreeing closely together, which have even smaller pinnae than those above mentioned and no trace of subapical contraction. They differ from the smallest specimens of *L. leptocarpa* (those from Borneo) in having shorter pinnae, less acuminate, and on shorter stalks. Though they differ very much from typical *L. cochinchinensis*, I do not know where else to refer them, and with some doubt include them here; they may represent a reaction to environmental conditions. Possibly further collections may resolve the difficulty, especially if young plants can be found. The three specimens are: Clemens 22000 from Sarawak, Valeton 191 from Java (the only specimen of this species from Java, except cultivated ones) and Versteeg 1183 from New Guinea.

It is interesting to note that the characteristic features of *L. cochinchinensis* (as of *Teratophyllum gracile*) are most markedly developed by young plants; old plants may have narrower tapered pinnae and even perhaps approach *L. leptocarpa,* but young plants of the two species are very different, those of the latter having very narrow acuminate simple fronds.

In the Malay Peninsula *L. cochinchinensis* is typically a fern of rather wet lowland forests, though not so abundant in the very swampy localities as *Teratophyllum ludens.* Young plants may fairly often be found; they sometimes creep along the ground, or on rocks by streams, and may so attain a size sufficient to bear fertile fronds, but the largest plants are always found climbing trees to a considerable height.

Specimens seen.

MALAY PENINSULA. *Singapore*: Bukit Timah, Ridley s.n. 1894, s.n. 1900 (HS); Botanic Gardens, Holttum 17484 (HS). *Johore*: G. Pulai, Hullett s.n., 1880 (HS); S. Sembrong, Holttum 24972 (HS); S. Endau, Holttum 24946 (HS). *Selangor*: Ginting Sempak, 1500 ft., Hume 8572 and 9365 (FMS Mus); Telok Forest Reserve, Holttum 19872 (HS). *Pahang*: near Bukit Sagu, Henderson 25082 (HS); S. Cheka, Corner 24872 (HS); Mentakab, Holttum 24557 (HS); Sedagong, P. Tioman, 800 ft. Henderson 18618 (HS); Fraser's Hill, 3500 ft., Holttum 11360. *Perak*: Larut, 300 ft., King's Collector 4205 (HS); Upper Perak, 300 ft., Wray 3703 and 3624 (HS). *Penang*: Curtis 1718 (HS). *Kedah*: P. Langkawi, Holttum 17439 (HS).

SUMATRA. Lebong Tandai, Benkoelen, C. J. Brooks 236 S (HB); 151 S (HC). Lalah, Indragiri, Burchard 81 and 132 (HCal).

BORNEO. *Sarawak*: Bishop Hose s.n., 1894 (with juvenile plant of *Teratophyllum aculeatum,* HS); Gat, Upper Rejang River, J. & M.S. Clemens 22000 (HCal). *Dutch Borneo*: Pladjoe, Amdjah 118, 119 (*S. abrupta* v.A.v.R., HB, HCal); Teuscher s.n. (HB).

JAVA. Noesa Kembangan, Valeton 191 (HB). Cult. in Hort. Bot. Bog. II K (IX, 10) (HB).

CERAM. Amahey, Treub s.n. 1893 (HB). Below 300 m., Rutten 1919 (HB).

NEW GUINEA. Versteeg 1183 (HB). von Rohmer 101 (HB). K. Wilhelmsland, Sattelberg, 600–700 m., Bamler (HCal; *Sten. Bamleri* Ros. MS, Fil. novoguin. exsic. no. 251). Papua, Rev. C. King 1913 (HCal; named *Sten. Kingii* Copel. by Rosenstock).

2. **Lomariopsis Smithii** Fée, Hist. Acrost. 71; t.33 f.29, t. 53 (1845).

Stenochlaena longifolia J. Sm. 1841 (nomen).

In his citation of this species, Fee states " Habitat in Mauritio (Commerson, Herb. Paris) et in Ins. Philipp. (Cuming). Exsiccatum: Cuming no. 143." Underwood makes no reference to Mauritius in referring to this species, and evidently regards Cuming's specimen as the type; in this I follow him, as Cuming's specimen is the only one precisely cited. It is unlikely that the Mauritius plant is the same.

In Copeland's herbarium is a specimen of the type collection of *L. Smithii.* In habit and general appearance it is closely similar to *L. cochinchinensis,* but differs very strikingly in having long-stalked pinnae (stalks to 15 mm. or more long); the pinnae also do not show the abrupt contraction just below the apex, and they are rather narrow at the base, but these characters may also sometimes be found in *L. cochinchinensis.* The fertile pinnae are 5 to 7 mm. wide. Examination of other Philippine specimens shows that plants exist which are more or less intermediate between Cuming's plant and the typical form of *L. cochinchinensis.* Of Elmer's 13893, the specimen in the Buitenzorg Herbarium quite closely resembles Cuming's but that in Copeland's Herbarium is much more like typical *L. cochinchinensis* in all the characters mentioned. It appears likely that young plants of *L. Smithii* (as of *L. cochinchinensis*) bear fronds the pinnae of which have shorter stalks, broader bases, and more abruptly contracted apices than the pinnae of fronds on older plants; but I am not sure that this would account for all the variation, and field study of the species is needed. One can find fronds of adult plants of *L. cochinchinensis* which agree quite closely with typical *L. Smithii* except for the character of the stalks of the pinnae. It is interesting to note that *L. subtrifoliata* and *L. oleandrifolia* are distinguished in the same way (the former having almost sessile pinnae and the latter very long stalked ones), and show no other clear differences.

Specimens seen.

PHILIPPINES. *Luzon*: Cuming 143 (HC); Cagayan Prov., Ramos 13887 (HC); Casiguran, Tayabas Prov., Ramos & Edano 45245 (HC, HM, HCal); Ponawa River, Camarines Sur, Edano 76519 (HCal, HM); Los Banos (Mt

Maquiling), Elmer 17997 (HB, HC); Rizal Prov., Loher 14795 (HCal, HM). *Mindanao*: Cabadbaran (Mt Urdaneta) Angusan Prov., Elmer 13893 (HB, HC). Copeland's specimen from Mt. Matutune 4000 ft. (HC no. 12232) has sessile pinnae and rather resembles the type of *L. Kingii.*

3. **Lomariopsis intermedia** (Copeland) Holttum, *comb. nov.*

Stenochlaena intermedia Copeland, Philip. Journ. Sci., 7C, 67(1912). *Original description*: Rhizomate ca. 1 cm. crasso, basique stipitis paleis atrocastaneis 15 mm. longis, 1.5 mm. latis sat dense vestito et deinde ob baseos duras spiniformes earum horrida; stipite 40 cm. vel alto, valido, sursum rhichique paleis latioribus vestitis et haud spinescentibus; fronde 60 to 70 cm. alta, pinnata, pinnis ad rhachin articulatis; pinnis utroque latere ca. 8, frondis sterilis subsessilibus, basi plus minus obliquis, rotundato-truncatis, apice abrupte breviter caudatis, 20 ad 22 cm. longis, 45 ad 55 mm. latis, integris, papyraceo-coriaceis, glabris, venis liberis; frondis fertilis pinnulis stipitatis (stipitibus 4 ad 8 mm. longis), 15 ad 20 cm. longis, 2 mm. latis, sursum sensim angustatis.

PAPUA. Ambasi, King 370.

Only the original collection is known; this I have seen. It is a very large fern, allied to *L. cochinchinensis.* A few points in the description call for comment. The stipe and rachis are very stout, the stipe of the dried frond being nearly 1 cm. in diameter and the middle of the rachis 6 to 7 mm. The pinnae are large, very broad (the apical pinna 5.5 cm. broad), with the abruptly contracted apex of *L. cochinchinensis*, but decidedly thicker in texture than is normal for that species. The most remarkable feature of all is the fact that the fertile pinnae are up to 2 cm. broad (not 2 mm. as in the description) and are completely covered with sporangia. This is certainly a very distinct species.

4. **Lomariopsis leptocarpa** Fee, Hist. Acrost. 69, t.29 (1845).

Lomaria spectabilis Kze, Bot. Zeit. 1848, 144.

Lomariopsis spectabilis Mett., Fil. Lips., 22(1856).

Acrostichum spectabile Racib., Pterid. Buitenz., 54 (1898).

Stenochlaena leptocarpa Und., Bull. Torr. Bot. Cl. 33, 47(1906).

The type of this species is Cuming's 132 from Luzon. I have not seen this, and among the specimens from Luzon which I have examined none are fully adult. There are however many fine adult specimens from Java; they agree well with Fee's figure and were referred to *L. leptocarpa* by Underwood. The specimens from Luzon have mostly simple or trifoliate fronds, but the largest frond of Edano 79645 has six pairs of pinnae and is sufficiently large for a comparison with the Java specimens, with which it agrees closely. In my opinion there can be little doubt that the plants from Java and the Philippines are all referable to the same species; if it should become necessary to distinguish the Java plants, the name *L. spectabilis* would have to be revived for them. The following description of adult plants is taken from Java specimens; that of young plants from Philippine and Sumatran material.

Young plants have at first narrow simple fronds, the largest 30 cm. long and only 1.2 cm. wide, with stipe 5 cm. long (Edano 77968). The fronds are narrowed gradually to base and apex. Later fronds have one or more pairs of pinnae below the terminal pinna, the rachis more or less narrowly winged. Bornean specimens also agree in these characters.

Adult plants have fronds to at least 70 cm. long, with 15 or more pairs of pinnae. The rachis is more or less flattened and narrowly winged towards the apex; the pinnae are subcoriaceous, to about 20 cm. long by 1.5 cm. wide (occasionally as large as 25 by 2 cm.), the base narrowly slightly unequally cuneate, the sides almost parallel for the greater part of their length, the apex acuminate, margins entire or tending to be sinuate towards the apex, veins 1.5 to 2 mm. apart; the lower pinnae with stalks up to about 1 cm. long; fertile pinnae about 4 mm. wide and up to 24 cm. long.

Elmer's 11788 from Mindanao differs somewhat, the sides of the pinnae being less nearly parallel and the veins closer together. The Clemens collection from B.N. Borneo also differs, the pinnae being very long-acuminate and the veins less than 1.5 mm. apart; the fronds are also rather small, the largest pinna 16 cm. long. It is possible that such differences may be due to conditions of growth (greater or less shade or moisture). The Clemens collection is rather similar to the three odd specimens mentioned under *L. cochinchinensis,* but differs in the pinnae being more acuminate and longer stalked. The young plants however indicate quite clearly its relationship with *L. leptocarpa* and not with *L. cochinchinensis.*

DISTRIBUTION. Philippines, Borneo, Java, Sumatra.

Specimens seen.

PHILIPPINES. *Luzon*: Tamdagan River, Cagayan Prov., Edano 79652 (HM, HCal, HC); Pakigpik, Cagayan

Prov., Edano 79645 (HM, HS, HC). *Palawan*: Mt. Gantung, Edano 77968 and 77972 (HM, HC). *Mindanao*: Todaya (Mt Apo), district of Davao, Elmer 11788 (HC).

JAVA (all HB). Tjibodas, 1700 m., Raciborski s.n., Arsin 19629, J. J. Smith s.n. 1906, Sapiin 2716 (HCal), Bruggeman 259. G. Poentjak, Hallier s.n. 1895. G. Tikoekoer, 1450 m., Backer 12841. G. Halimoen 1400–1500 m., Backer 10941. Rawa Tjankoewang, Scheffer 2. M. Tiloe, Scheffer 16583. M. Malawar, Scheffer s.n. 1871. Tjilaket, Mousset 917. Pasoeroean, Tangkil, Koorders 2355 b. (HCal).

SUMATRA. G. Dempo, 3500–4000 ft. (also sterile at higher altitudes), C. J. Brooks 15898 (HB). Brastagi, 4800 ft., Corner 25315 (HS).

BORNEO. Dallas-Tenompok ridge, Kinabalu, 4000 ft., J. & M. S. Clemens 27596; climbing to 30 ft. on small trees; some fertile fronds only 3 ft. from the ground.

5. **Lomariopsis Raciborskii** (C. Chr.) Holttum, *comb. nov.*

Acrostichum Smithii Racib., Bull. Int. Ac. Cracovie 1902. p. 59.

Stenochlaena Raciborskii C. Chr., Ind. Fil. 18, 625 (1905).

Raciborski's original description of this species (as *Acrostichum Smithii*) is very detailed. He cites the locality and type as follows: "Molukken. Buitenzorger Garten no. 277b." This appears to indicate a cultivated specimen. I have examined specimens of plants cultivated at Buitenzorg and referred to this species but there is nothing to indicate that any one of them is the type. Raciborski's description may be summarised as follows. Frond with three pairs of lateral pinnae; the lateral pinnae articulated, but not the terminal one; the lateral pinnae sessile, 13–20 cm. long by 2.2–3 cm. wide, long acuminate, "dunkelgrün, glänzend, hart, brüchig;" the terminal pinna 25–30 cm. long; lateral veins at right angles to the costa or slightly ascending, 1 mm. apart, simple or forked; fertile pinnae 2.5–5 mm. wide; in the rachis 5 vascular bundles, higher up 4 only, in the pinnae two vascular bundles. Raciborski finally remarks "Diese Art ist von den bekannten Stenochlaena-arten leicht wegen der kleinen zahl der Blättchen eines Blattes zu unterschieden. Ausserdem fehlen dem *Acr. Smithii* die fein zerschlitzten sterilen Blätter, wie solche bei *A. aculeatum*, *gracile* und wahrscheinlich mehrere anderen Formen der variablen Gruppe des *A. sorbifolium* vorhanden sind." This again is evidence of the absence of dissected bathyphylls in Lomariopsis, though Raciborski evidently did not recognise the distinction between Lomariopsis and Teratophyllum.

Though fertile fronds were present, it is unlikely that Raciborski's specimen represented the fully grown adult form of the species; possibly the conditions of cultivation induced the premature formation of fertile fronds. In v. A. v. R.'s *Supplement*, p.428, is the statement "pinnae plurijugate in the adult plants." The largest specimen in the Buitenzorg herbarium has six pairs of pinnae; the pinnae are broadest near the base and gradually narrowed to their long-acuminate apex. The plants are somewhat similar to those of *L. cochinchinensis* which lack the abruptly contracted apex to the pinnae; the pinnae of *L. Raciborskii* however are decidedly more acuminate and more coriaceous than those of *L. cochinchinensis,* while they differ from those of *L. leptocarpa* in being broader, shorter-stalked, and in having veins closer together. Further material of this species from the Moluccas is needed in order to show the true adult form of the plant under natural conditions, and its range of variation.

The specimens are: Cult. in Hort. Bog. II. K (V) 23, II. K (XIV) 41.

6. **Lomariopsis Kingii** (Copeland) Holttum *comb. nov.*

Stenochlaena Kingii Copeland, Philip. Journ. Sci. 6C, 80(1911). *Original description.* Lomariopsis, caule 1 cm. crasso, inerme, paleaceo; stipite non articulato, 20 cm. longo, plaeaceo deinde glabrescente; pinnis frondis sterilis multijugis, ca. 16 cm. longis, 20–22 mm. latis, brevissime stipitatis, articulatis, basi cuneatis, acuminatis, crenulatis, coreaceis, glabris, siccis supra atroviridibus, infra olivaceis; pinnis fertilibus 20 cm. longis, 2 mm. latis, stipitibus earum 5 mm. longis, validis.

Ambasi, Papua, Copland King no. 285.

I have examined the type (in HC). The aspect is somewhat between *L. leptocarpa* and *L. cochinchinensis.* The pinnae are almost sessile, quite narrowly cuneate at the base, broadest rather above the middle; the edge is slightly crenulate, but little more so than is occasionally seen in *L. leptocarpa;* the veins are closer than is usual in *L. leptocarpa.* The pinnae are more like those of *L. Raciborskii,* but their shape is rather different, being broadest rather above the middle instead of near the base. The very narrow fertile pinnae of *L. Kingii* are probably characteristic; those of *L. Raciborskii* are considerably wider.

var. petiolulata Rosenstock MS.

In the California herbarium is a specimen bearing the above name, which I believe has not been published. The specimen agrees quite well with the type of *L. Kingii,* except that the pinnae are rather long-stalked (5 mm. or rather more) and have sides rather more parallel. The upper pinnae have broadly cuneate to rounded bases, but the lower ones have narrower bases; the upper pinnae are absent from the type specimen of *L. Kingii,* so that a comparison on this point is not possible. The fertile pinnae are very narrow, as in the type of *L. Kingii.* For the present this form may reasonably be ranked as placed by Rosenstock, but it is possible that further collections may indicate the desirability of separating it specifically.

Type specimen: NEW GUINEA, Sattelberg 300 m., Bamler no. 50.

7. **Lomariopsis novae-caledoniae** Mett., Ann. Sc. Nat. IV, 15, p.58 (1861).

Stenochlaena novae-caledoniae Und. Bull. Torr. Bot. Cl. 33, 49(1906).

This species appears only to be known from New Caledonia. I have seen two sheets of the collection specified below. The rhizome is typical of Lomariopsis. The fronds have almost sessile pinnae, about 15 mm. wide, rather similar to those of *L. leptocarpa* but with a crenulate edge. The fertile pinnae are 1 cm. broad. These characters adequately distinguish *L. novae-caledoniae* from *L. leptocarpa,* which apears to be its nearest relative.

Specimens seen. NEW CALEDONIA. Yahoué, 200 m., Franc 663 (HB, HCal).

8. **Lomariopsis subtrifoliata** (Copeland) Holttum, *comb. nov.*

Stenochlaena subtrifoliata Copel., Philip. Journ. Sci. 1, Suppl. 152(1906). *Original description.* Rhizomate scandente, 10–15 mm. crasso, angulato; paleis fuscis lanceolatis vel ovatis 5–10 mm. longis densissime vestito; stipitibus 10 20 cm. longis, validis, deorsum perpaleaceis, sursum subglabrescentibus; fronde plantae adultae pinnata 45–70 cm. longa, ovata; pinnis ad rhachin articulatis, superioribus sessilibus plerumque obliquis, inferioribus stipitatis, ca. 25 cm. longis, fertilibus 10 mm. sterilibus 25–30 mm. latis, acutis vel caudatis,integerrimis margine cartilaginea, coriaceis, glabris; venis omnino liberis, conspicuis; sporangiis .5 mm. longis, paginam totam margine costaque exceptis inferiorem complentibus.

Mindanao, Zamboanga, San Ramon, Copeland 1749. Ad truncos scandente, 750 m. s.m.

Copeland adds: " The fronds of young plants are simple, a gradual change to the pinnate form occurring long before maturity. So far as *Gymnogramme ? (Syngramme ?) subtrifoliata* Hooker in Sp. Fil. 5, 152, pl. 298, ever was described, it is indistinguishable from this Stenochlaena." However, when he came to deal with the ferns of Fiji, he stated (p.65) under *S. oleandrifolia* " I suppose this is also *Gymnogramme subtrifoliata* Hooker." Copeland's *S. subtrifoliata* was found in the Philippines, and a number of other collections, clearly identical, have also been made in those islands. *S. oleandrifolia* from Fiji differs from the Philippine fern very constantly in the possession of very long stalks to the pinnae though in other respects the two are very closely allied. If we are to keep them as distinct species, as I consider justifiable, then the name *Gymnogramme subtrifoliata* (given by Hooker to an immature plant from Fiji) is a synonym of *S. oleandrifolia* Brack. (an older name) and not of *S. subtrifoliata* Copel.

L. subtrifoliata is well described in the diagnosis above quoted. It and *L. oleandrifolia* agree is being very stout and coriaceous, the fronds drying to a pronounced dull olive brown colour, different from that of all other species of Lomariopsis I have examined. The pinnae of *L. subtrifoliata* are almost sessile, the longest stalks seen being barely 5 mm. long, whereas those of *L. oleandrifolia* are constantly very much longer. In a genus such as this, where specific differences are slight, such a constant distinction seems to me a sound basis for specific distinction. As remarked above, however, one would like to know what kind of plants grown in the intervening geographic region.

Specimens seen:

PHILIPPINES. *Mindanao*: San Ramon, Zamboanga, 2500 ft., Copeland 1749 (type, HC); Mt. Matutune, Copeland s.n. May 1917 (HC). *Leyte*: Dagami, Ramos 15261 (HC). *Luzon*: Irosin, Mt Bulusan, Sorsogon, Elmer 16318 (HB). *Samar*: Catubig River, Edano 24756 (HB).

9. **Lomariopsis oleandrifolia** (Brack.) Mett., in Kuhn, Verh. zool bot. Ges. 19, 571 (1869).

Stenochlaena oleandrifolia Brack., Expl. Exp., 16, 75 (1854).

Gymnogramme ? (Syngramme ?) subtrifoliata Hook., Sp. Fil. 5, 152, t.298 (1864).

Lomariopsis Seemanni Carr., in Seemann, Fl. Vitiensis, 373 (1873).

I have not seen the originals of any of these species, but I have seen all the specimens quoted by Copeland (Ferns of Fiji, p.65). They agree together very closely. The specimens of Gillespie's no. 2144 and 2119 in the Herbarium of the University of California are labelled *S. Seemanni,* but they do not differ from the other specimens labelled *S. oleandrifolia.* The identity of these two species can only be decided by comparison of the types; it seems highly probable that they are identical.

The type of Hooker's *Gymnogramme subtrifoliata* was Milne's no. 108 from Naviti Levu, Fiji. It is an immature specimen with only one pair of lateral pinnae, which are almost sessile. It is probable that the long stalks characteristic of pinnae of adult plants are not developed by young plants, and that young plants of *L. subtrifoliata* and *L. oleandrifolia* are very similar to each other. The two species are clearly very closely allied, and the only definite distinction between them is in the length of the stalks of the pinnae; in *L. oleandrifolia* the upper pinnae have stalks about 1 cm. long and the lower pinnae have stalks 2.5 to 3.5 cm. long.

10. **Lomariopsis Brackenridgei** Carr., in Seemann, Fl. Vit. 373 (1873).

Stenochlaena Brackenridgei Und., Bull. Torr. Bot. Cl. 33, 45 (1906).

Of this species I have seen the specimens quoted by Copeland in his paper on the Ferns of Fiji (p.66). The rachis is slender, the pinnae distant and narrowly cuneate at the base, and the fertile pinnae very narrow. The most characteristic feature is the long stalks of the pinnae (stalks of lower pinnae about 15 mm. long). Copeland regards as typical of the species a specimen with pinnae to 15 by 2.5 cm. Their aspect recalls that of *L. cochinchinensis,* but they are firmer and on much longer stalks. They are broader in proportion to their length than the pinnae of *L. leptocarpa,* and the veins are closer and more clearly defined. Copeland also mentions a narrow serrulate form which is connected with the typical form by intermediates. This narrow serrulate form has pinnae 16 cm. by 1.4 cm., which except for the serrulation (the teeth are rounded) is very near *L. leptocarpa* in appearance. In fact there is as much difference between the two forms as there is between most recognised species of Lomariopsis.

11. **Lomariopsis Setchellii** (Maxon) Holttum, *comb. nov.*
Stenochlaena Setchellii Maxon, Univ. Cal. Publ. Bot. XII (1924).

The type of this species is from Tahiti. I have not seen it, but have seen another specimen referred to this species in the California herbarium. The rhizome is normal for Lomariopsis, the stipe and rachis stout, the pinnae closely placed, subsessile (stalks less than 3 mm.), about 1.8 to 2 cm. wide, the texture decidedly thin, the base narrowly unequally cuneate.

I have also seen a specimen from Samoa which is quite similar, but has much longer pinnae. Further material may show the distinctness of the Samoa fern, but on the basis of the present specimens no definite distinguishing characters can be established.

Specimens seen:

TAHITI. Vaearaia, 170 ft., M.L. Grant 3974 (HCal).

SAMOA. Olonono, Savaii, Vaupel ?, 20.1.1905 (HC).

TERATOPHYLLUM Mett.

Kuhn in Ann. Mus. Lugd. Bat. IV, p.296 (1869).

The type species of Teratophyllum is *T. aculeatum* (Bl.) Mett. As explained above, this species was based on Blume's *Lomaria aculeata,* and was construed as including all ferns with specialised bathyphylls. Kuhn included in the same species *L. gracilis* Bl., and in the var. *inermis* he included all immature specimens having an unarmed rhizome under three headings: nos. 1 and 2 are evidently *T. ludens* (*Lomariopsis ludens* Fée) and no. 3 includes all the very young dimidiate stages of *T. aculeatum* proper. The collections of recent years have demonstrated the existence of several distinct species of Teratophyllum. Some of these are now fairly completely known, but others still need further investigation in the field, and possibly more are yet undiscovered. One species, *T. luzonicum,* is only known from one collection of adult fronds.

The ferns of this genus are all very closely allied together. The following are the characters which seem to be common to all of them. The rhizome is slender and climbing (sometimes creeping in its young stages) usually more or less aculeate, dorsiventral, rooting on one side and with two rows of leaves on the opposite side, more or less covered with small ciliate peltate scales, which are lost by old rhizomes (fig. 31) ; similar scales are found on the rachis and leaf surfaces. The leaf bases on the rhizome are swollen and partially articulated. The rhizome contains on the ventral side a vascular bundle which is almost divided into two halves, like the basal bundle in Lomariopsis; in addition to this it has one dorsal bundle only (fig. 23). Bathyphylls are borne on the lowest part of the plant, both on the earliest stems and on the numerous

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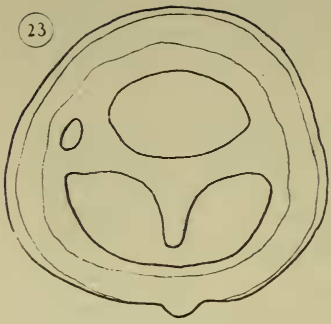

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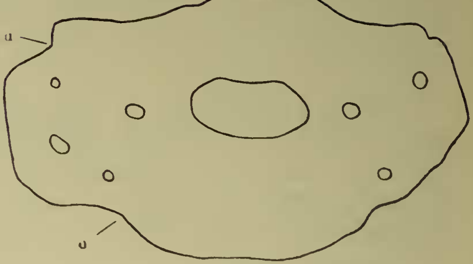

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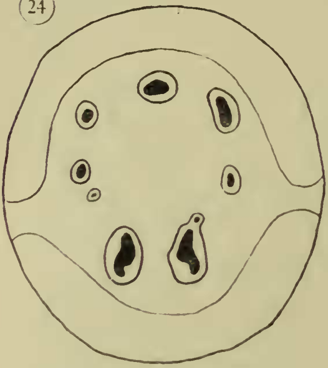

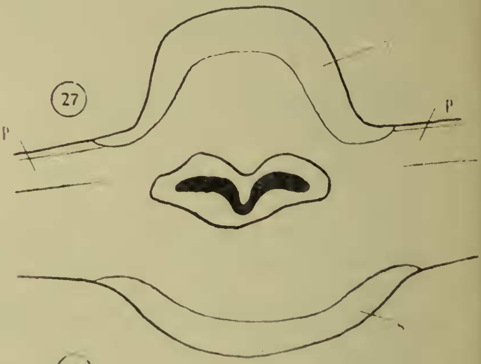
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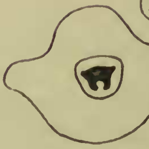
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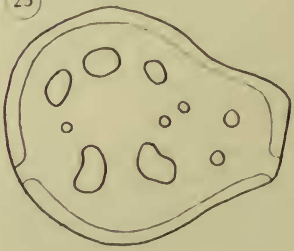

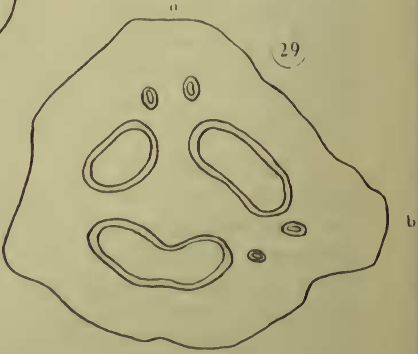
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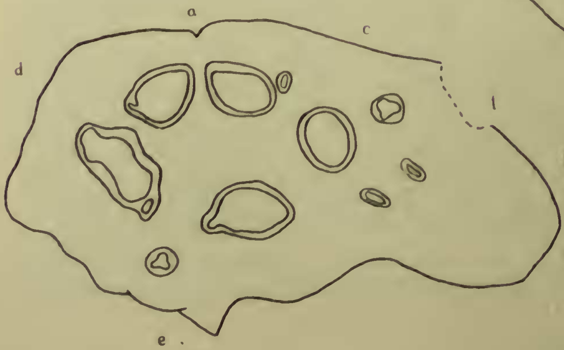
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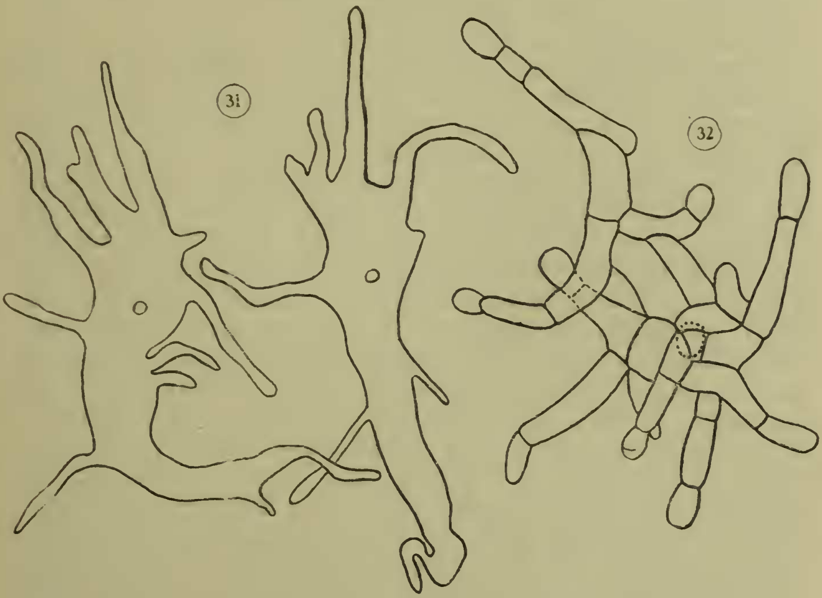
later branches which arise near the ground. Bathyphylls have a great variety of form; all agree in bearing numerous minute scales like those on the rhizome, in having the lower pinnae at least articulate and the lowest pinnae always turned down at right angles to and overlapping the rhizome. The adult sterile leaves have all their pinnae articulate; their stipes contain an open ring of several vascular bundles, as in Lomariopsis (fig. 24). The fertile leaves are always acrostichoid and have usually very narrow pinnae; *T. rotundifoliatum* is an exception, and to a lesser extent *T. arthropteroides.* The spores are large, 80 x 50μ or more exclusive of the large convoluted perispore (fig. 4,5).



31, *Teratophyllum ludens*, scales from base of stipe, x 60.
32, *T. aculeatum*, scale from bathyphyll, x 220; the circle represents the point of attachment.

23–28, *Teratophyllum ludens.* 23, t.s. rhizome. 24, t.s. stipe (xylem black). 25, t.s. rachis just below pinna. 26, t.s. pinna stalk. 27, t.s. sterile pinna; ss, sclerenchyma; pp, palisade tissue. 28, t.s. fertile pinna; from *a* to *a* is the soriferous surface. 29–30, *Asplenium epiphyticum.* 29, t.s. rhizome; a, b, bases of next two leaves. 30, t.s. same rhizome, a little higher than fig. 29; a & b indicate same positions on rhizome (a is now above the last leaf); b,c,d,e, indicate bases of next leaves in order; roots are being produced at e & f. 23–26, x 12. 27–28, x 33. 29–30, x 11.

The morphology of the leaves of Teratophyllum is a matter of considerable interest. The fact that all pinnae are articulated is their characteristic feature, and one in which they constantly differ from Lomariopsis, which has always the terminal pinna continuous with the rachis. Some plants of Teratophyllum have leaves which are intermediate between the adult leaves and the typical bathyphylls; these transition leaves also have all the pinnae articulate and all about equal in size. If we trace the series back to the normal bathyphylls, we find that these are gradually attenuated to the apex, the upper pinnae becoming smaller and smaller and the uppermost not articulated; the rachis is continuous right to the apex of the frond without any articulation. There seems to be quite a sharp distinction between these bathyphylls with the uppermost pinnae gradually diminishing in size and losing their articulation, and the transition leaves (some of which are incised like the bathyphylls) and adult leaves which have all the pinnae subequal and all articulate. I have found no definite intermediate stages between these two types of leaf. I suggest however that in the transition and adult leaves the apex is suppressed, and that all their pinnae are really lateral, though one of them may occupy an approximately terminal position (it often happens that no pinna is clearly terminal). The species *T. ludens*, in which the " all lateral " stage is very early developed, appears to show occasionally what may be vestiges of the frond apex, but further microscopic examination is needed before a definite pronouncement can be made. There are other ferns which have all pinnae articulated on adult fronds; two I have noted in particular are *Lomagramma perakensis* and one at least of the Peninsula ferns commonly referred to *Cyathea moluccana*. I have examined plants of the Lomagramma from the youngest stage upwards; they never show a stage like that of the bathyphylls of Teratophyllum, but have almost from the beginning a small number of definitely separate pinnae, all the pinnae becoming articulated on very early leaves, the apical pinna included. It seems that in Lomagramma the apex of the frond is definitely cut off from the rachis by an articulation, and there is no evidence whatever that the apex is aborted. In the Cyathea the position is much less clear. Plants with leaves up to about 20 cm. or more long have the rachis continuous with the leaf apex and the upper pinnae gradually diminishing in size. I have not been able to examine enough transition stages to understand clearly the way in which the change to the adult condition takes place, but I think it possible that here also the leaf apex is aborted as in Teratophyllum. The articulation of pinnae has evidently developed independently in several fern stocks, and one may expect the details of its occurrence near the frond apex to vary with different forms of fronds.

The bathyphylls of Teratophyllum may be classified developmentally in various more or less distinct stages; these stages are used in the descriptions of the species which follow. The *earliest stage* is that in which the leaf lamina is lobed, and not divided into distinct pinnae. The *dimidiate stage* (where present) is that in which the fronds bear pinnae on the lower side of the rachis only. The term *normal bathyphylls* is applied to those fronds which have pinnae equally on both sides, and in which the upper pinnae are gradually smaller in size, the frond apex not being articulate. Bathyphylls in which the pinnae are all articulate, are called *transition bathyphylls;* they are usually dissected like the other bathyphylls, but sometimes are partly or wholly webbed, in which condition, except as regards size, they closely resemble the adult leaves. A young plant bears first the early stages up to normal bathyphylls; stouter branches from the base of an old plant bear at once normal bathyphylls or transition bathyphylls. In *T. aculeatum* var. *montanum* the form of the bathyphylls is apparently related to the conditions under which the plant is growing. In *T.ludens* and *T. Koordersii* the normal bathyphyll stage is omitted, and only transition bathyphylls, having all the pinnae articulated, are found; some of the transition bathyphylls are even dimidiate.

All species of Teratophyllum grow in moist shady forest; never in exposed places of the kind in which *Stenochlaena palustris* flourishes. The individual species differ somewhat in their habitats; for example, *T. ludens* grows only in swampy forest or wet valley bottoms, where the ground is constantly wet, whereas *T. rotundifoliatum* grows on sloping ground well above the valley bottoms. The bathyphylls of all species agree in this, that they always and only grow in the lowest stratum of the forest, within a few feet of ground level. Karsten in 1895 described the bathyphylls of a Teratophyllum from the Moluccas. He found that they adhered closely to the supporting tree trunk, that they had little or no cuticle, and suggested that they served a water absorbing function. I have particularly noted the habit of growth of the bathyphylls of a number of plants of Teratophyllum, and find that in the youngest stages of *T. aculeatum* the bathyphylls do not adhere to the supporting tree but stand out away from it on the lower side of their rachis, thereby exposing their surface more effectively to the light. I have also described under *T. aculeatum* and its variety *montanum* how some of the larger bathyphylls also hold their leaflets away from the tree trunk, while others cling closely to it. My impression is that in the darkest and dampest situations the bathyphylls do not adhere closely to the tree trunks, but that in more open and lighter situations (as on a hill slope or ridge) the pinnae of the bathyphylls do adhere to their support; and that within a species there may be variation in this matter. *T. rotundifoliatum*, growing as I have seen it on upper valley slopes in Johore, had all its pinnae closely appressed to the tree trunks; in herbarium specimens of this species one may note that there is no overlapping of adjacent fronds, whereas in *T. aculeatum* adjacent fronds which are not when living wholly appressed to the supporting tree overlap when pressed for the herbarium.

As regards the function of the bathyphylls, there can be no doubt that they are capable of absorbing water. I recently performed a simple experiment on this matter at Cameron's Highlands. I took a few bathyphylls, all from the same rhizome, and air dried them (not in the sun) for 24 hours, by which time they were shrivelled. I then took one of them and put the apical ⅓ of it into water in a tumbler, the basal part not being immersed. In a few hours the apical part of the frond was again turgid, though the lower pinnae remained shrivelled; it therefore appears that the absorption of water was not very considerable. The exact measurement of the intake of water of such leaves under natural conditions would be a difficult matter, and at present one can only guess what their activity may be. All the old plants with tall climbing stems which I have examined have had quite large root systems in the soil, and did not appear to stand very considerably in need of additional water absorption through the leaves.

The distribution of the species of Teratophyllum is interesting. *T. aculeatum* covers practically the whole range of the genus, so far as it is at present known, from Sumatra to New Guinea and the Philippines. It is a lowland species, except that the mountain plant of the Malay Peninsula and Sumatra is here reckoned as a variety of it. Co-existing with *T. aculeatum* in the lowlands of the Malay Peninsula, Sumatra and Borneo in *T. rotundifoliatum;* in the Malay Peninsula is also *T. ludens;* in Celebes is *T. Koordersii*, and in the Philippines *T. Williamsii*, *T. arthropteroides* and *T. luzonicum*. There may be other distinct lowland species still to be discovered; Borneo and New Guinea have so far yielded very few specimens of the genus. On the mountains of Java is the very uniform and distinct *T. gracile*, the adult form of which is very similar to that of *T. aculeatum* v. *montanum*.

Every one of these species (except *T. luzonicum* of which only the adult from is known) is distinct throughout its various stages and can be recognised equally well either from bathyphylls or from adult fronds. Below are given two keys, one based on bathyphylls only and the other on the adult leaves only. From the former key I have omitted *T. arthropteroides,* as I have not seen its bathyphylls. These keys are not separately infallible; but, if both bathyphylls and adult leaves are available, a doubtful identification from one key may be checked by the other.

Keys to the species of Teratophyllum

1. *Bathyphylls*

  1. Pinnae deeply incised 2
  1. Pinnae at most crenate 5
  2. Pinnae up to 7 or 8 mm. wide, pinnules with few segments 3
  2. Pinnae up to 1.5 cm. wide, pinnules with several segments on each side 4
  3. Segments of pinnae rounded, youngest fronds not dimidiate *T. rotundifoliatum*
  3. Segments of pinnae linear, youngest fronds dimidiate *T. aculeatum*
  4. Segmentation of pinnae lax, ultimate divisions usually 2 to 3 mm. long *T. Williamsii*
  4. Segmentation of pinnae closer, ultimate divisions rarely 2 mm. long *T. gracile*
  5. Pinnae very unequal at the base *T. Koordersii*
  5. Pinnae almost equally cuneate at the base *T. ludens*

2. *Adult leaves*

  1. Basal pinnae on stalks less than 7 mm. long 2
  1. Basal pinnae on stalks at least 7 mm. long 6
  2. Bases of pinnae very unequal 3
  2. Bases of pinnae not very unequal 4
  3. Pinnae subcoriaceous, edge entire *T. Koordersii*
  3. Pinnae of thin texture, edge crenulate *T. arthropteroides*
  4. Pinnae 2 to 4.5 cm. wide, elliptical *T. ludens*
  4. Pinnae 1 to 2.5 cm. wide, sides parallel for about half their length 5
  5. Pinnae usually 1 to 1.5 cm. wide, texture firm, drying red* *T. gracile*
  5. Pinnae usually 2 to 2.5 cm. wide, texture thin, not drying red *T. aculeatum*

6. Fertile pinnae 1 cm. wide *T. rotundifoliatum*
6. Fertile pinnae 2 to 3 mm. wide 7
7. Pinnae to 2 cm. wide, on stalks to 7 mm. long, drying red *T. Williamsii*
7. Pinnae to 3 cm. wide, on stalks to 12 mm. long, not drying red *T. luzonicum*

*Specimens of *T. aculeatum* v. *montanum* may agree on these points with *T. gracile*, but may be distinguished by their bathyphylls.

1. **Teratophyllum aculeatum** Mett.; Kuhn in Ann. Mus. Lugd. Bat. 4, 296 (1869). Pl. 2 & 3.

Lomaria aculeata Bl., Enum. 205 (1828).

Stenochlaena aculeata Kze, Bot. Zeit. 1848, p.142.

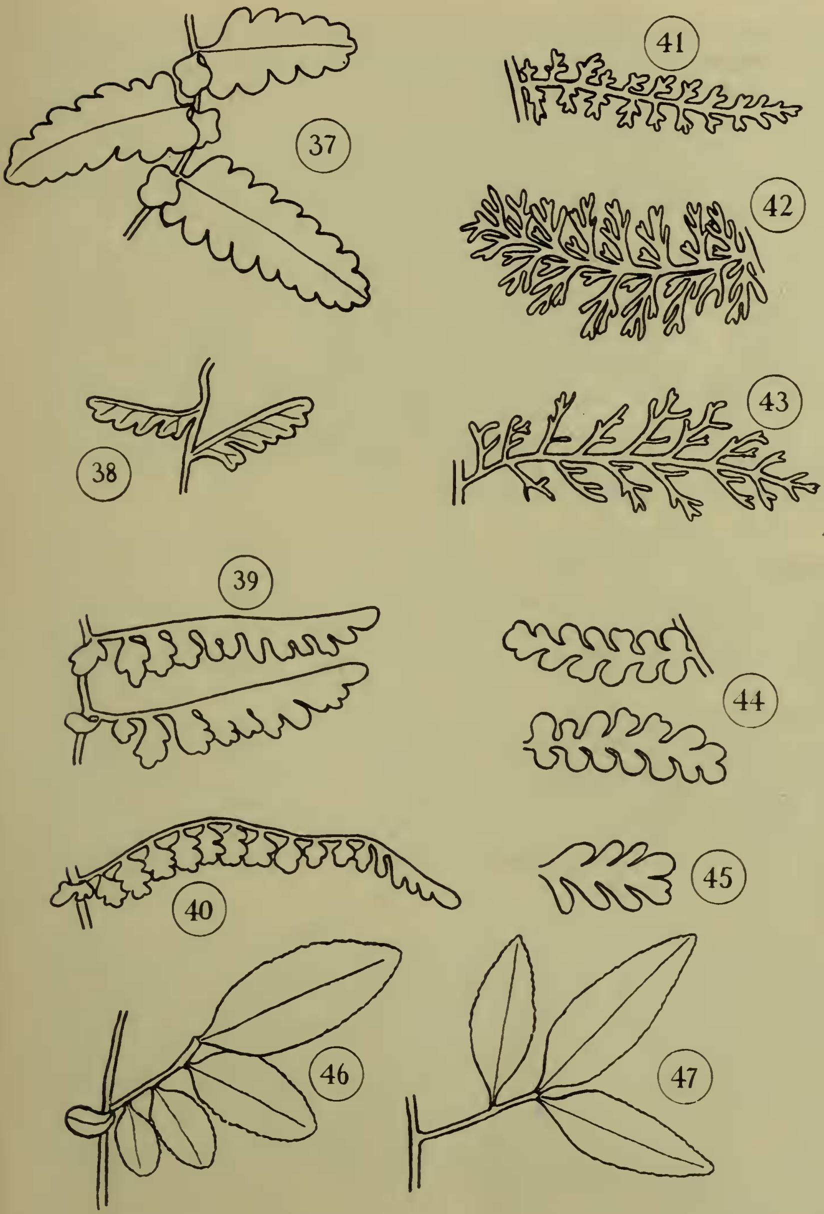
Lomariopsis spinescens Fée, Acrost. 71, tab. 33 f. 1 (1845).

Davallia achilleaefolia Wall.; Hook., Sp. Fil. 1, 195, t.56D. Bedd., F.B.I., t.209.

Blume originally described this species very briefly under the heading *Lomariae dubiae;* he evidently considered the bathyphylls as fertile leaves. I have not seen the type specimen, but I have seen several other specimens from Java, which agree well with plants from the Malay Peninsula. The following detailed description is based on the ample material from the Peninsula in the Singapore Herbarium, and on my own field notes.

The characteristic features of the species are: early stages dimidiate; normal bathyphylls with pinnules simple or forked, about 1 mm. wide; adult sterile pinnae subsessile, 9–10 by 2–2.5 cm., base broadly cuneate, texture thin; fertile pinnae very narrow.

Dimidiate stage (figs. 38–40). Rhizome of very young plant slender, creeping or climbing; leaves quite dimidiate, broadest at the base and gradually tapering to the apex, the upper edge perfectly straight, the lower edge broadly lobed, the basal lobes deepest and separating at an early stage as separate pinnae, the lowest lobe or pinna deflexed and overlapping the rhizome. Successive leaves have more and more lobes separated as distinct pinnae, but the leaves remain quite dimidiate up to at least 7 cm. long by 9 mm. or more wide at the base. The pinnae of such leaves may be 20 or more, the apical ones coalescing,



Bathyphylls of Teratophyllum spp. 37, youngest stage of *T. rotundifoliatum*, showing single basal pinnae overlapping the rhizome. 38, youngest stage of *T. aculeatum*. 39, a later dimidiate stage of *T. aculeatum*. 40, largest entirely dimidiate stage of *T. aculeatum*. 41, *T. aculeatum* v. *montanum*, pinna of the largest bathyphyll seen.

42, *T. gracile*, pinna from bathyphyll. 43, *T. Williamsii*, do. 44, *T. rotundifoliatum*, do. 45, *T. aculeatum*, a common form of pinna.

46, *T. ludens*, bathyphyll from a climbing stem. 47, *T. ludens*, a small bathyphyll from a creeping stem. 37–45, all about x 1½ 46–47, x $\frac{2}{3}$

the lower ones articulate and often somewhat overlapping. The lower pinnae are lobed, sometimes only half way to the costa, more often leaving only a narrow costal wing; the largest pinnae at this stage are about 9 by 6 mm., with 4 or 5 lobes on each side, the width of the lobes varying but usually barely 1 mm. Some fronds of this type have pinnae as broad as long (on one frond the pinnae are 6 by 6 mm.) and shallowly lobed. The larger and later fronds of this type have lobes beginning to develop on the upper edge, starting from the apex and in later leaves gradually extending towards the base. These form a transition to the normal bathyphylls. In climbing, plants, the leafless upper edge of the rachis of dimidiate leaves is pressed closely to the supporting tree trunk, the pinnae, on the side towards the ground, standing out a little distance away from the support. These fronds never lie flat against a vertical tree trunk.

Normal bathyphylls. These also vary vey much in the fineness of their ultimate divisions. The largest are usually about 9 by 2 cm. (some from the Philippines are 12 by 5 cm.), and their pinnae up to 11 by 5 mm. The pinnae have about 5 segments on each side, the segments 1 mm. wide, or a little more, some being forked (fig. 45). The lower pinnae are the largest, and the higher pinnae are gradually reduced in size, the uppermost ones not being articulate. The rachis is usually winged throughout. Stomata are few, and are scattered irregularly over the surface. I have not observed the distribution of stomata described by Karsten (near the edges of the segments and not near the veins).

Transition bathyphylls. In these leaves all the pinnae are articulate and subequal, the apex of the frond being apparently suppressed. Finely dissected fronds of this nature appear to be rarely developed in the typical form of this species, though they are common in the *var. montanum* described below. Hume's no. 7947 from Selangor has fronds 14 by 7 cm., pinnae up to 18 pairs, the largest pinna about 4 cm. by 8 mm., the pinnules up to 12 pairs on one pinna, each pinnule with 2 to 4 linear segments, these segments not usually more than 2 mm. long and 0.5 mm. wide.

More frequently are found transition bathyphylls which have a greater or less degree of webbing between the ultimate segments, thus showing a more complete transition to the simple entire pinnae of normal adult fronds, though the size of the fronds is usually much less. Corner's specimen from the Mandai Rd. Singapore has transition fronds only about 8 by 3 cm. Holttum's 10632 from Johore has similar fronds 18 by 6 cm. In both these cases the lowest pinnae turn towards and cross the rhizome, as in all bathyphylls.

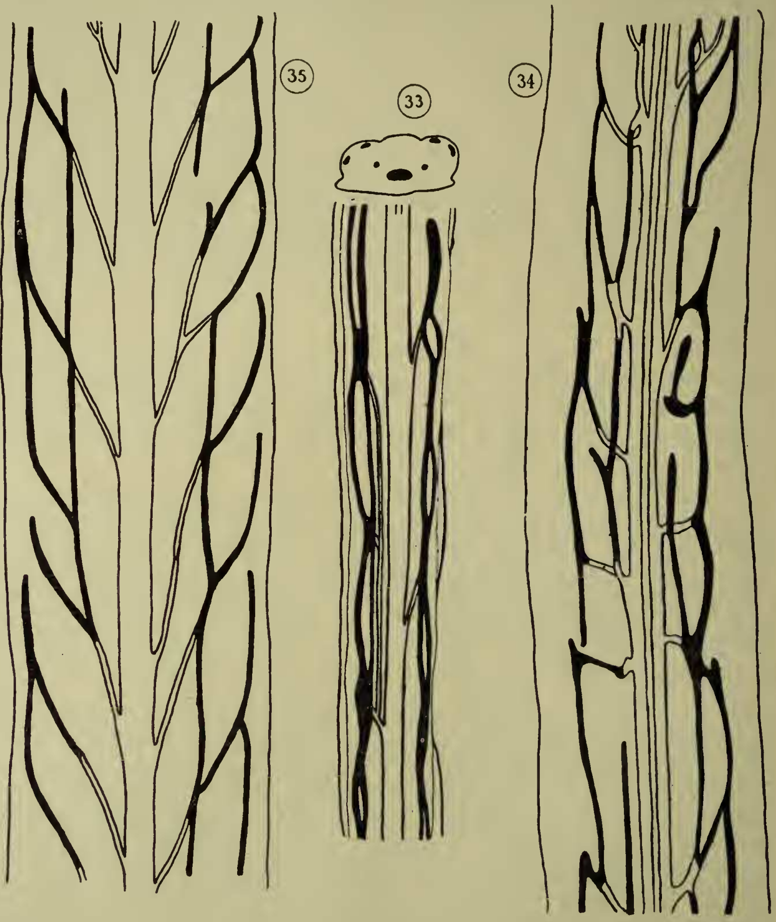
Adult sterile leaves. These are usually about 40 cm. long by 16 cm. wide, with 16 or more pairs of pinnae. The pinnae are almost sessile, about 9 or 10 cm. long and 2 to 2.5 cm. wide, broadly cuneate or rounded to subtruncate at the base, the sides parallel in the lower half, and then tapering gradually to the apex. Holttum's 10632 from Johore has pinnae to 16 by 2.5 cm., but some fronds of the same collection have pinnae only 8 by 1.8 cm. Fronds of this species sometimes show a tendency to reddening, though usually they do not (this character is in fact a very dubious one for diagnostic purposes; see remarks under *var. montanum*). The texture is thin, and both surfaces are usually more or less thickly scattered with minute brown scales of the same kind as on other parts of the plant.

Fertile fronds. These have very narrow pinnae, sometimes less than 2 mm. wide. Their substance is comparatively thick, and they have a peculiar venation illustrated in fig. 33, p. 288. Fertile fronds of this species have rarely been collected.

The typical *T. aculeatum* is a lowland fern which extends throughout the Malayan region, from Sumatra to New Guinea and the Philippines. In the mountains of Java is *T. gracile*, clearly allied but quite distinct in young and adult stages from typical *T. aculeatum* (unfortunately the youngest stages are still unknown). In the mountains of Sumatra and the Malay Peninsula however is a fern which connects typical *T. aculeatum* with *T. gracile*, agreeing very nearly with the former in its bathyphylls and with the latter in its adult stage. Under these circumstances it is difficult to decide how to classify these ferns. On account of its very distinct bathyphylls I have decided to maintain *T. gracile* as a separate species; if its youngest stages prove equally distinct, that will definitely confirm the separation. The mountain fern of Sumatra and the Malay Peninsula however is so much nearer to *T. aculeatum* (its bathyphylls are not definitely distinguishable and its adult fronds sometimes approach *T. aculeatum*) that I am classing it as a variety of that species, var. *montanum*.

A specimen from Borneo (exp. Nieuwenhuis, coll. Jaheri, no. 35), in the Buitenzorg herbarium, quoted by Christ (1906(2), p.119) under *Lomariopsis sorbifolia* (another sheet of the same collection is illustrated by Christ in 1906 (1), taf. 3) has peculiar bathyphylls. On the Buitenzorg specimen all bathyphylls have entire pinnae.

The fronds range from 10 by 3 cm. down to 5 by 1 cm., and the pinnae from 2 cm. by 9 mm. to 5 by 3 mm.; the pinnae have broadly rounded apex and base, and entire or minutely crenulate margins. All fronds have pinnae on both sides of the rachis. On the sheet figured by Christ are younger dimidiate fronds of a common type; the bathyphylls with entire pinnae may probably be regarded as



Venation of fertile pinnae of Teratophyllum, from below, the superficial veins shown black. 33, *T. aculeatum*, with diagrammatic transverse section, x 9. 34, *T. aculeatum v. montanum*, x 11. 35, *T. ludens*, x 11.

premature transition leaves, possibly caused by environmental conditions. The present material is insufficient to establish these specimens as a distinct variety, but further collections might show that such a variety exists. In any case, much more remains to be discovered about the Teratophyllum species of Borneo.

Specimens seen.

MALAY PENINSULA. *Pahang*: S. Cheka, Corner 24497 (HS); Mentakab, Holttum 24551 (HS); Joara Bay, P. Tioman, Burkill s.n 1915; Lubok Lanun, P. Tioman, Henderson 18861 (HS, HB, HCal); Tahan River, Ridley s.n. 1891 (HS). *Singapore*: Mandai Rd. Corner 24498 (HS); Bukit Panjang, Ridley s.n. 1906 (HS); Bukit Timah, Md Nur s.n. Feb. 1931 (HS); Herb. Hullett, s.n. 2 sheets (HS). *Johore*: Ulu Kahang 400 ft., Holttum 10632 (HS, HB); Ulu Madik, Holttum 10632 A (HS); foot of G. Panti, Holttum 17699; G. Pulai, Hullett s.n. Aug. 1880 (HS). *Malacca*: Jus, Goodenough 1464 (HS). *Selangor*: Petaling 10th mile, Ridley s.n. 1889 (HS); Kotan Tunggal Reserve, Hashim s.n. 1908 (HS); Ulu Langat, Goodenough s.n. 1896; Ginting Sempak 1500 ft. Hume 9458 (FMS Mus.); Semenyih, Hume 7947, 7975 (FMS Mus.); Bukit Kuda, Ridley s.n. 1889 (HS); Klang Gates, Hume 7253 (FMS Mus.); Woods, Batu Caves, Ridley s.n. 1896 (HS). *Perak*: Kellas Estate, Ipoh, Fox s.n. 1899 (HS); Ulu Bubong 300–500 ft., Kunstler 10, 005 (HS); Gopeng, Kunstler 1117 (HS). *Peninsular Siam.* Pungah, Curtis s.n. Feb. 1893 (HS).

SUMATRA. Sawak Mts. 2700 ft. Forbes 1933c (HS); Tebing Tinggi, 100 m. Lörzing 7439 (HB). Djambi Res., 140 m. Posthumus 898 (HB).

BATOE ISLANDS. Raap, 147 (HB).

BORNEO. Jaheri s.n. 1893 (HB); G. Kenepai, Hallier s.n. 1852 (HB); Semedoem, Hallier 667; foot of G. Damoes, Hallier 440 (HB).

JAVA. Pasoeroean, Tangkil-Zuidergebergte, 400–500 m., Koorders 23598b; Kali Klepoeh, Res. Besoeki, Gandrup s.n. June 1929 (HB); foot of G. Lamongan, Res. Pasoeroean, Zollinger 2303 (HB); Pasir Tjihideung, Res. Batavia, 600 m., Dakkus 187 (HB); Zollinger s.n. 1842–8 (HCal as *Stenochlaena gracilis*); von Goebel s.n. (HCal. no. 391653).

PHILIPPINES. *Luzon*: Botol River, Camarines Sur, 2200 ft., Edano 76528 (HM, HC); Rizal Prov., Loher 14073 (HM, HCal); Los Banos (Mt. Maquiling), Laguna Prov., Elmer 17966 (Hcal, HC). *Mindanao*: Misamis Prov., Miranda 20279 (HC).

NEW GUINEA. Lam, 424, 1105 (HB); Damun, Werner 64 (HCal).

T. aculeatum var. **montanum**, *var. nov.* Pl. 1 & 4.

This variety is found on the mountains of the Malay Peninsula and Sumatra. Typical adult leaves are hardly distinguishable from the adult leaves of *T. gracile* from Java, but the bathyphylls have very short pinnules, and sometimes approach closely those of the typical lowland *T. aculeatum.*

Normal bathyphylls. On slender young stems these have usually rather broad segments to the pinnae, very much as in typical *T. aculeatum.* This condition is shown in Henderson's 17739 from Cameron's Highlands, which has the segments of the pinnae simple or forked only, the ultimate divisions about 1 mm. wide. I have seen such plants growing in the valley forest at Cameron's Highlands and also at Fraser's Hill; the rachis of the fronds and the pinnae of the upper side are pressed closely against the tree trunk, while the pinnae of the lower side stand out away from the trunk, their surfaces facing a little skywards. The fronds are often so close together that when pressed flat they overlap. I have also found bathyphylls on stout creeping and climbing rhizomes, in more exposed positions on ridge slopes in the forest, the pinnae of which are much more finely dissected, and all of them lying close against the tree trunk (or against the ground in the case of creeping stems). Such bathyphylls may have the ultimate segments only about 0.2 mm. wide. There are other specimens in the Singapore Herbarium more or less intermediate between these two extremes, and I believe that environment has a good deal of influence on the form of the bathyphylls. The largest normal bathyphylls seen are those of Burkill's 12986 from Birch's Hill (fig. 41); these are 16 cm. long by 4.5 cm. wide, the largest pinna 2.5 cm. long by 6 mm. wide, with 12 pairs of pinnules; the apical pinnules simple, to about 1.5 by 1 mm., the largest pinnules 3.5 mm. long by 2.5 mm. wide, with forked apex and 2 or 3 lateral ranches, the largest segments about 3 mm. long by 0.5 mm. wide. Lorzing's specimen from Sumatra agrees.

Transition bathyphylls. On Holttum's 23364 from Cameron's Highlands and s.n. from Fraser's Hill are transition leaves up to 22 cm. long by 9 cm. wide, with 20 pairs of pinnae; the pinnae are only 5 mm. wide, and are partially dissected.

Adult sterile leaves. These are usually about the same size as those of typical *T. aculeatum,* but with narrower pinnae. The pinnae are usually 10 to 12 cm. long and 8 to 15 mm. wide. One Fraser's Hill specimen has pinnae to 14 by 2 cm., and Wray's no. 712 has pinnae to 16 by 1.5 cm., but these are apparently exceptional. In Corner's collection from Brastagi, some fronds have rather small pinnae, others up to 15 by 1.8 cm. The texture is possibly a little firmer than that of the lowland plant. The pinnae of *var. montanum* are nearly always dark green when dry, but sometimes a little reddish; the midribs and rachis are nearly always pink or red, though occasionally not so. I have seen no fronds with quite the deep shade of the specimens from the mountains of Java (*T. gracile*). It appears however that the degree of redness depends partly on the conditions of drying. The base of the pinnae of *var. montanum* is usually broadly rounded to truncate, the lower side being narrower than the upper. The plants from the Taiping Hills however have at least the lower pinnae quite narrowly cuneate, though the bases of the higher pinnae may be broader; this may constitute a local race. The specimens from the Main Range of the Peninsula usually agree with those from the neighbourhood of Brastagi in Sumatra.

Fertile leaves. The pinnae are very narrow, and are quite similar to those of typical *T. aculeatum.* The lamina is thickened, and the vascular arrangement is approximately as figured. There is a series of areolae formed by superficial veins or trachied masses close to the lower surfaces, and these areolae are supplied by branches from the midrib bundles, which lie at a level nearer the upper surface of the frond (fig. 34, p. 288).

Specimens seen.

MALAY PENINSULA (all HS). *Perak*: Taiping Hills 3500–4000 ft., Kunstler 8309; Birch's Hill 3800 ft., Burkill 12725, 12986; Maxwell's Hill, Wray 712, Ahmad s.n. 1895, Fox 116; Sungei Sengam, Holttum 24998. *Pahang*: Cameron's Highlands, 4800 ft. Henderson 17739, Holttum 23364; Fraser's Hill, 4000 ft., Burkill & Holttum 8459, Holttum s.n. March 1929, Henderson 11428, Md Nur 11114. *Selangor*: Semangkok Pass, Ridley s.n. 1904.

SUMATRA. O. Sibayak 1400 m., Lörzing 8658, 8669 (HB); Brastagi, 4800 ft. Corner 25316 (HS).

2. **Teratophyllum gracile** (Bl.) Holttum *comb. nov.* Pl. 5.

Lomaria gracilis Blume, Enum. 205 (1828).

Stenochlaena gracilis Kze, Bot. Zeit. 1848, p.142.

Acrostichum gracile Raciborski, Pterid. Fl. Buitenz. 53 (1898).

This species was briefly described by Blume; he distinguished it from his *Lomaria aculeata* by its purpurascent adult fronds and its finely divided bathyphylls with narrow linear segments. There is a fine series of specimens in the Buitenzorg harbarium; all are from the mountains of the west of Java, and all agree closely together. One important item of information concerning them is lacking; the youngest stage is not represented in the collections, and there is no example of dimidiate fronds. It would be very interesting to know whether in the early stages this species agrees with *T. aculeatum.* The essential features of *T. gracile* may be described as follows.

Bathyphylls. These are all of relatively large size, and are all of the type with all pinnae articulate which I have called transition bathyphylls. The largest seen are about 16 cm. long by 7 cm. wide, with 12 to 15 pairs of pinnae, the largest pinnae about 4 by 1.5 cm. with 12 pairs of pinnules, the largest pinnules having 4 segments (some forked) on each side and a forked apex, the ultimate segments rarely 2 mm. long and usually about 0.3 mm. wide (fig. 42, p. 285). These fronds are thus very similar to those of *T. Williamsii,* but they have closer and smaller ultimate divisions. As the pinnae of these bathyphylls may be 1.5 cm. wide, a complete webbing would give them at once the form of adult leaves. Such webbig, complete or partial, does occur in some pinnae of occasional bathyphylls; other pinnae of the same fronds may be fully dissected.

Adult sterile leaves. These may be 40 cm. long by 15 cm. wide, with up to 15 pairs of pinnae; the pinnae are about 8 to 10 cm. long by 1 cm. wide, or exceptionally 1.5 cm. wide, more or less abruptly and broadly cuneate to subtruncate at the base, texture thin but firm, drying dark red in all cases.

Fertile leaves. The fertile pinnae are up to about 10 cm. long and are 1 to 2 mm. wide.

Specimens seen.

JAVA (all HB). G. Beser, Tjidadap, Tjibeber, 1000 to 1400 m., Winckel 10 b, Bakh. v.d. Brink 2426, 2403, 3878, 3946, J. J. Smith 737, Backer 22674; G. Karang, Tjidadap, Tjibeber, 1000 m., Bakh. v.d. Brink 835, Winckel 837 b; Tjadasindlang (?), 1000 m.. Winckel 1516 b, 1713 b; Tjiharoen bij Tjibeber, Docters van Leeuwen-Reijnvaan 2389; G. Malang, Raciborski s.n. (HCal); Tjihandjawar bij Wandjar, Bakh. v. d. Brink 4342; Nanggerang, Backer 8722 (HCal).

3. **Teratophyllum Williamsii** (Underwood) Holttum *comb. nov.* Pl. 6.

Stenochlaena Williamsii Und., Bull. Torr. Bot. Cl. 33, 41(1906).

S. gracilis var. *Williamsii* v.A.v.R., Supplement 431.

The type of this species is Williams no. 684 from the Lamao river, of which I have seen a fragment from Copeland's herbarium. I have also seen several other specimens from the Philippines. The species appears to occur in the low country. In all specimens the youngest stage is missing, so that no information is available as to the presence or absence of dimidiate fronds.

Normal bathyphylls. One specimen shows these. They are about 4 cm. long by 2.5 cm. wide, with about 8 pairs of pinnae, the highest pinnae progressively smaller and the lowest one crossing the rhizome at right angles. The larger pinnae have about 4 pairs of pinnules, and the largest pinnules have about 4 lateral segments, the segments to about 3 mm. long and 0.5 mm. wide.

Transition bathyphylls. These differ from those of *T. gracile* in their more lax branching and longer ultimate segments. The largest frond of this type seen is about 12 cm. long by 6 cm. wide, with 9 pairs of pinnae, the largest pinna 3.5 by 1.5 cm. with 7 pairs of pinnules, the larger pinnules each having about 3 to 4 linear lateral segments and a forked apex, the segments 2 to 3 mm. long and about 0.3 mm. wide (fig. 43, p. 285). Some of these bathyphylls have some pinnae with the lamina partly webbed. On a sheet of Copeland's no. 2044 are two small transition leaves about 8 cm. long, pinnate right down to the rhizome, the pinnae to 18 by 5 mm., almost entire except the lower ones which are incised.

Adult sterile fronds. These are as much as 50 cm. long and have up to about 12 pairs of pinnae. The texture of the pinnae is thin and firm, about the same as *T. gracile*. The pinnae are up to 20 cm. long by 2 cm. wide (sometimes only 10 by 1.5 cm. or even smaller), widest near the base and tapering gradually to an acuminate apex; the base is not quite equal (more narrowly cuneate on the lower side) narrowly to rather broadly cuneate. The lower pinnae at least are on rather long stalks (to 7 mm. long), a distinction form *T. gracile*. The leaves when dry are usually pink or reddish, especially the midribs of the pinnae. The bathyphylls are sometimes reddish, sometimes not.

Fertile leaves. Underwood states that the pinnae of fertile leaves are twice as long as sterile pinnae. This statement is true of the type but not of several other specimens I have seen. The specimen of Copeland's no. 2044 in the Singapore Herbarium has fertile pinnae rather shorter than the sterile ones; that in Copeland's Herbarium has longer fertile pinnae but still not twice as long as the sterile ones. Elmer's no. 12543 has fertile pinnae at least 27 cm. long, and Reillo's no. 15403 25 cm. The fertile pinnae are very narrow, as in *T. aculeatum* and *T. gracile*, being usually less than 2 mm. wide when dried.

Specimens seen.

PHILIPPINES. *Luzon*: Lamao R., alt. 400 ft. Williams 684 (type; fragment in HC); Mt. Caboloan, Cagayan Prov., Edano 78738 (HM); Paningtingan, Rizal Prov., Loher 13514 (HM); Lamao R., Bataan Prov., P. T. Barnes 68 (HC); Mt. Mariveles, 600 m., Copeland 2044 (HS, HC). *Panay*: Capiz Prov., Edano 46118 (HM, HCal). *Sibuyan*: Magellanes (Mt. Ginting-Ginting), Capiz Prov., Elmer 12543 (HB, HC). *Basilan*: *Reillo* 15403 (HC).

4. **Teratophyllum rotundifoliatum** (R. Bonap.) Holttum *comb. nov.* Pl. 7, 8.

Stenochlaena rotundifoliata R. Bonap., Notes Pterid. 14, 58 (1923).

S. aculeata var. *crassior* v.A.v.R., Bull. Btzg. 1916, XXIII, pp. 20–21.

This species was described from a specimen (G. Lambak, Johore, Holttum 9384) bearing bathyphylls and very small fronds of adult type. *S. aculeata v. crassior* was described from a specimen from southern Sumatra consisting of transition bathyphylls and adult leaves not quite fully expanded. I have recently found in southern Johore a locality where plants showing all bathyphyll stages (including the *v. crassior* stage) and adult sterile leaves were growing near together, some plants showing on the same stem two or more stages of development. I have seen the type of *v. crassior*, and find it quite identical with these Johore specimens. There is also a fine series of specimens from Perak, collected by Wray. These show the distinctive bathyphylls, adult fronds (some of which are rather different from those of the Johore plants; for discussion see below), and most remarkable fertile fronds. I consider that these Perak plants are conspecific with the Johore plants, and that we have thus available specimens of this species showing all stages from the youngest onwards.

The distinctive features of the species are: earliest leaves not dimidiate, bathyphylls with more or less rounded ultimate segments, adult sterile fronds with coriaceous pinnae on long stalks, fertile pinnae broad, with a dual vascular system. Bonaparte was wrong in saying that the species differs from *T. aculeatum* in having the ends of the veins free from the edge and thickened; *T. aculeatum* agrees in this.

Youngest stage (fig. 37, p. 285). Leaves simple, to about 2.5 cm. long and 7 mm. wide, the apex rounded, the margins lobed, the lobes rounded and 2 to 3 mm. wide and deep, the base unequal, the lower side with a large auricle overlapping the rhizome, the upper side cuneate. Texture thin but rigid. The largest leaves of this type have the basal auricle separated as a distinct pinna. These leaves occur only very close to the ground, on tree roots and the bases of tree trunks.

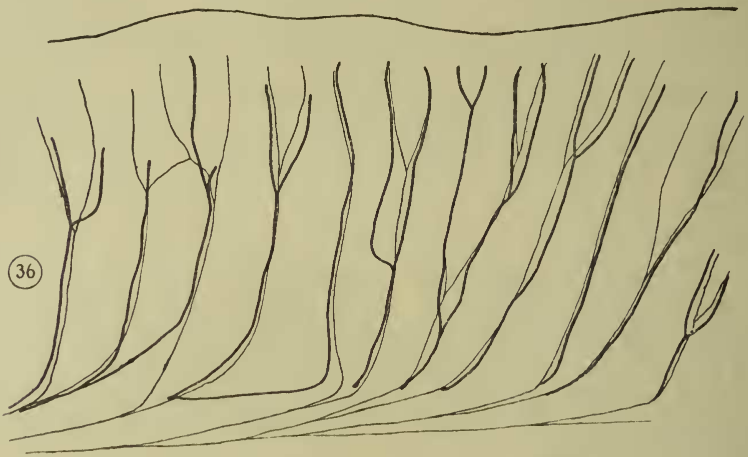
Normal bathyphylls (fig. 38, p. 285). The smallest of these are only 15 by 3 mm.; the largest are up to 8 cm. long by 3.5 cm. wide, the pinnae closely placed, the lower ones largest and articulate, the upper ones progressively smaller towards the apex, the largest pinnae about 15 by 4 mm., pinnate at the base, the pinnules usually almost circular (on the largest fronds the pinnules have the apex retuse or more deeply cleft), veins in the pinnules simple or forked, usually not very prominent above and sometimes hardly visible superficially, ending some distance short of the margin; texture firm (stiff and brittle when dry); both surfaces scattered with the usual minute brown scales. Some bathyphylls dry red, but others do not.

Transition bathyphylls. These have been found 11 to 15 cm. long by 4.5 to 6 cm. wide, and with 15–20 pairs of pinnae. The pinnae are separated by about their own width, and their texture is decidedly coriaceous; they are up to about 3 cm. long by 4 mm. wide, deeply lobed throughout, the lobes nearly all retuse or sometimes trilobed; both the surfaces are scaly.

Adult plant. The rhizome is stout and sharply aculeate, to 8 mm. in thickness when dry, when young covered with a very dense felt of fibrillose red-brown scales of the type usual in this genus, but larger than those seen in any other species. Some of the scales on young fronds are at least 7 mm. long by 1 mm. wide, dark in colour with a paler edge; there are other scales intermediate between them and the usual small scales.

Sterile fronds. These may be 60 cm. long (including stipe) by 30 cm. wide, with at least 12 pairs of pinnae; the largest pinnae about 15 cm. long by 3 cm. wide, broadest one-third from the base, gradually tapering to the apex, the base rather broadly cuneate, the texture coriaceous, veins prominent on both surfaces, terminating just within the margin. All pinnae have long stalks; the stalks of the lowest pinnae are 10 to 15 mm. long. The sterile fronds on one of Wray's specimens from Perak have rather few large pinnae, up to 16 by 6 cm., but the fronds are on thin rhizomes and evidently represent a not fully adult state. On another sheet is a somewhat larger frond with pinnae up to 12 by 4 cm. The plant from Matang, Sarawak, is similar. From Gunong Angsi also are fronds of adult type but from small plants. These fronds are about 30 cm. long with pinnae 8 by 3 cm.; apparently young plants (or possibly plants in deeper shade) tend to have proportionately broad pinnae. The pinnae of dried fronds tend to be rather pale in colour.

Fertile fronds. These are only known from Wray's collection, and in a rather young state (though fully expanded) ; the sporangia are immature. These fronds are up to 70 cm. long by 20 cm. wide, with about 14 pairs of pinnae, the pinnae up to 10 cm. long by 1 cm. wide, on stalks to 18 mm. long. The venation is of a dual nature. There are separate veins close to the lower surface, more or less parallel to the normal veins, but not strictly so; examination of a cleared pinna with a binocular microscope shows clearly that these two sets of veins lie at different levels. A drawing of the venation is shown in fig. 36. This peculiar venation is related to the unusual width of the lamina, as compared with other species of the genus; it represents a modification of the venation found in *T. aculeatum* adapted to the wide pinna of *T. rotundifoliatum.* I suggest that it is an indication that the widening of the fertile pinnae in *T. rotundifoliatum* is a secondary development, and that the narrow pinnae of *T. aculeatum* are the primitive form in the genus.



36, fertile pinna of *Teratophyllum rotundifoliatum* (half width), from below, the normal veins thinly drawn and the soral veins, close to the lower surface, thicker; x 15.

Dr. Posthumus's collections from Djambi, Sumatra, are of bathyphylls only. These have rather finer divisions than those so far found in the Malay Peninsula, but they are so similar in other respects that I think they must be referred to this species. Even the very smallest ones (only 1 cm. long) show no signs of a dimidiate condition. Of the larger fronds, the pinnae are only up to 8 mm. long by 2 mm. wide, with very small segments. Burchard's specimen from Indragiri, Sumatra, has exactly similar fronds, except that the lateral segments of the larger pinnae are bilobed instead of entire. The Sarawak collection of J. & M. S. Clemens has unusually large bathyphylls, with pinnae to 3 cm. long and 6 mm. wide, the segments proportionately large but in form identical with that of Peninsular specimens. The Java specimen quoted is slightly doubtful. It is a rhizome carrying a fine series of normal bathyphylls, the segments of which are somewhat intermediate between the forms typical of *T. aculeatum* and *T. rotundifoliatum.* Some of them show the almost round shape of the latter species, but others are more oblong. There are, however, no dimidiate leaves, and the texture and general appearance suggest *T. rotundifoliatum.*

Specimens seen.

MALAY PENINSULA. *Singapore*: Bukit Timah, Md Nur s.n. 1931 (HS). *Johore*: G. Lambak 1500 ft., Holttum 9384 (type collection, HS) ; S. Susur Rotan 500 ft., Holttum 24506 (HS). *Negri Sembilan*: G. Angsi, 2000 ft., Corner 24496 (HS). *Selangor*: Ginting Sempak, 1500 ft., Hume 9071 (F.M.S. Mus). *Perak*: Waterfall Hill, 2600 ft., Wray 679 (5 sheets in HS). *Penang*: Government Hill, Curtis s.n. 1890 (HS).

SUMATRA. Bengkoelen, Rimbo-Pangadang, 1000 m., Ajoeb 387 (type of *T. aculeatum v. crassior*, in HB). S. Merangin, Djambi, 180 m., Posthumus 903 (HB). Pad van S. Karing, Djambi, 180 m., Posthumus 743 (HB). Indragiri, in silvis pr. fl. Lalah ad arborum truncos, W. Burchard, 1907 (Dr. E. Rosenstock, Filic. Sumatranae exsic. no. 5, sheet in HCal; the left hand specimen only, the rest being *T. aculeatum*).

BORNEO. Matang, Sarawak, scandent on a rock face in forest, 1600 ft. J. & M. S. Clemens 22380 (HCal). Semedoem, Hallier 666 (HB).

JAVA. Preanger, Panjindangan, 600 m., Bakh. v. d. Brink 84 (HB).

5. **Teratophyllum luzonicum** Holttum *sp. nov.* Pl. 9.

Pinnae steriles longe (ad 12 mm.) petiolulatae, c. 15 cm. longae et 3 cm. latae, acuminatae, subcoriaceae; pinnae fertiles angustae (ad 3 mm. latae) ; bathyphylla ignota.

Rhizome about 4 mm. in thickness, somewhat aculeate, subglabrous when old. Stipes at about 5 cm. intervals on the rhizome, swollen and more or less articulate at the base, usually retaining numerous small scales. Frond, with stipe, to about 60 cm. long and 27 cm. wide, with at least 8 pairs of pinnae; pinnae to about 15 by 3 cm., on stalks up to 12 mm. long, broadly cuneate at the base, the sides nearly parallel, narrowed rather gradually in the distal $\frac{1}{3}$ of the pinna to an acuminate apex, the veins near the midrib about 1.5 to 2 mm. apart, usually forked once or twice and ending just short of the margin, prominent on both sides but more so on the lower surface; texture subcoriaceous; surfaces with scattered small scales. Fertile fronds to at least 27 cm. long by 17 cm. wide, pinnae up to 10 cm. long by 3 mm. wide, on stalks to 5 mm. long, their venation approximately as in *T. aculeatum* but modified somewhat owing to their greater width.

TYPE: Apayao Prov., Luzon, F. Fenix, Bureau of Science no. 28272. Specimen in Herb. Buitenzorg.

This species agrees very nearly with *T. rotundifoliatum* in the pinnae of the sterile adult leaves, in their long stalks, shape and texture, but the fronds of *T. luzonicum* are smaller and the pinnae are more acuminate. The fertile fronds of *T. luzonicum* are quite different from those of *T. rotundifoliatum*, having narrow pinnae, on shorter stalks.

T. luzonicum differs from *T. Williamsii* in the much broader pinnae, on longer stalks, drying green (even the midribs) not red. It may be rather closely allied to *T. Williamsii;* or the discovery of bathyphylls may show further differences.

6. **Teratophyllum ludens** (Fée) Holttum, *comb. nov.* Pl. 10.

Lomariopsis ludens Fée, Hist. Acrost. 70, t.30 (1845).

Lomaria limonifolia Wall. Cat. (1828) (*nomen*).

Stenochlaena limonifolia J. Sm., Journ. Bot. 4, 149 (1841) (*nomen*).

Teratophyllum aculeatum v. *inermis* Mett., Kuhn in Ann. Mus. Lugd. Bat. 4, 297 (1869): 1. folia subnormalia, et 2. folia anomala.

Beddome, F. B. I., tab. CCX.

John Smith's original name for this species was accompanied by no description; it rested on Wallich's specimen from Singapore, a photograph of which I have seen. Fée renamed the species, from collections of Gaudichaud from Singapore, and published a plate showing small adult fronds with only 5 pairs of pinnae and some of the bathyphylls; he does not illustrate fronds. Fée remarks of the species "elle est grimpante, et des frondules de presque toutes les formes se réunissent pour constituer des frondes, dont l'*habitus* varie a l'infini. Ces frondes, si elles étaient isolées, pourraient donner lieu a la formation d'espéces en apparence fort différentes les unes des autres." This great variety of form of the fronds is a constant feature of the bathyphylls of this species, which I have seen growing in a number of different localities. I have been able for the first time (apparently) to collect fully adult plants bearing fertile as well as sterile fronds, and give below a full description of all stages of growth of the species.

The characteristic features of the species are: earliest stage dimidiate; transition bathyphylls, appearing at a very early stage, all with crenate, not dissected, pinnae; bathyphylls of creeping stems with few pinnae, not dimidiate; bathyphylls of climbing stems dimidiate with small pinnae; adult sterile pinnae 7–12 by 2–4.5 cm., on stalks to 5 mm.; fertile pinnae narrow.

T. ludens grows in shady swamp forest or wet valley bottoms, and has only been found in the Malay Peninsula. Where it occurs it is usually very abundant, and it produces slender trailing stems which creep for long distances along the wet ground amongst roots and low undergrowth. These stems bear fronds of very variable form, which must be classed as bathyphylls. Where they climb the bases of tree trunks, the stems bear bathyphylls which are usually smaller and dimidiate. Though I have seen large quantities of this species in several localities it is only on rare occasions that I have noticed stems climbing any distance up the trunks of trees or bearing the fully adult type of frond; I have found the fertile fronds once only.

Youngest stage. No plants have been found showing both this stage and a more advanced one; the young plants here described were growing alongside typical plants of *T. ludens*, and I believe that they are to be referred to this species. They agree with the youngest fronds shown in Beddome's plate (two fronds at the bottom left-hand corner). The following is a description of young plants found at Mandai Road, Singapore: Rhizome very slender, creeping or climbing on tree roots in shady swamp forest. Leaves dimidiate, to 3 cm. long, narrowly winged throughout their length on one side, with a lamina up to 6 or 7 mm. wide on the other; lamina of the earliest leaves broadly lobed (the lobes deeper towards the base) and of later leaves the lowest 2 or 3 lobes almost or quite free, with crenate margins and subpinnate venation, the lowest lobe sometimes articulate. The terminal part of the these leaves is not articulate, and they resemble closely the earliest leaves of *T. aculeatum*.

Climbing stems with dimidiate or subdimidiate bathyphylls (fig. 46, p. 285). This stage follows closely upon the earliest stage just described, the difference being that here the apex of the frond is apparently suppressed and all the pinnae are similar and all articulate; all pinnae are still on one side of the rachis, except that one may occupy an approximately terminal position. The rachis is distinctly winged, and its upper side, devoid of pinnae, adheres closely to the tree trunk up which the plant is climbing, the pinnae being borne upon the lower side (i.e., that towards the ground) but standing obliquely outwards away from the trunk. Fronds of this kind are from 2.5 to 7.5 cm. long, with 5 to 9 pinnae, progressively smaller towards the base, the lowest overlapping the rhizome as do bathyphylls of other species. The pinnae are 5 to 30 mm. long, ovate, the base cuneate, the apex blunt, the edges entire towards the base and usually crenate towards the apex. The later fronds may have one or two pinnae on the upper side, towards the apex. On my no. 24904 are some small dimidiate fronds with the pinnae incised half way to the costa, but this is exceptional. In the same collection are dimidiate fronds 11 cm. long with pinnae up to 5 by 2.3 cm.; these seem to be intermediate between the normal small dimidiate climbing fronds and the adult type. In most cases however there is little transition between the small dimidiate leaves and the adult leaves (which of course stand out quite freely from the tree trunk) except that the lowest leaves of adult type are shorter and have fewer pinnae than the higher and later ones.

Trailing stems. The long trailing stems which are so abundant bear at rather long intervals paucipinnate fronds of varying size which are not usually dimidiate (fig. 47). The rhizome is slender and dark in colour. The stipes are articulate, 2 to 8 cm. long, winged usually to the base; the rachis is also winged. There are usually 2 to 4 pinnae, all articulate, lanceolate, up to 10 cm. long by 2 cm. wide, the edge distinctly crenate (occasionally subentire), widest ⅓ of the way from the base and narrowed gradually to the apex, the texture very thin. The size of these fronds, and of their pinnae, is very variable.

Adult plant. Rhizome about 3 mm. in diameter, not aculeate; the structure as in the other species of the genus (fig. 23, p. 278). Stipes about 5 to 10 cm. apart, on alternate sides of the rhizome, articulated and deciduous, swollen at the articulations, glabrous except when young, 5 to 20 cm. long, with about 8 vascular strands in an open ring (fig. 24). Young rhizome and fronds scaly, the scales brown, about 1 mm. long, base peltate, edges ciliate. Rachis pale, smooth, usually retaining scattered scales. not winged. Frond to about 45 cm. long and 25 cm. wide. Pinnae up to about 10 pairs, 2 to 4.5 cm. wide and 7 to 12 cm. long, the upper ones almost sessile, the lower ones on stalks to 5 mm. long, the base rather broadly and equally cuneate, narrowed gradually or rather suddenly to an acuminate apex; veins and midrib very prominent both above and below, veins simple or forked, 1 to 1.5 mm. apart, terminating just within the leaf margin; margin not thickened, somewhat inrolled in dried specimens, slightly sinuate; surfaces and veins when young rather thickly scattered with minute scales like those on the rhizome and stipe; old pinnae usually retain a number of these.

Fertile fronds. These are about the same size as the sterile ones. Fertile pinnae up to 20 cm. long and 3. mm. wide, usually on stalks about 5 mm. long. Lamina much swollen (see figure 28, p. 278 of transverse section) with a vascular system similar to that of *T. aculeatum* (fig. 35, p. 288).

Specimens seen. (all HS).

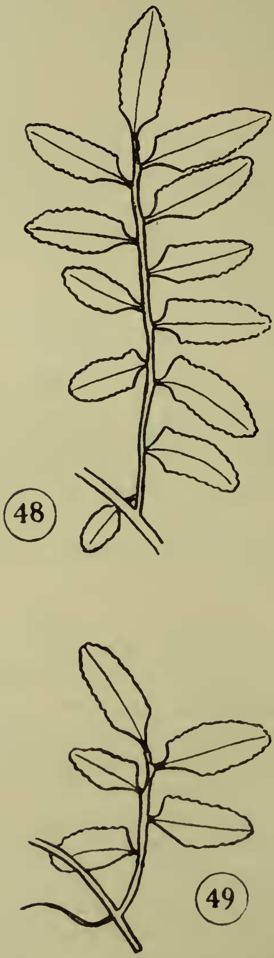
MALAY PENINSULA. *Singapore*: Mandai Road, Holttum 24632, 24795; Bukit Mandai, Ridley 1654; Bukit Timah, Holttum 24794. *Johore*: Mt. Austin, Ridley s. n.; G. Panti, 1500 ft., Holttum s. n.; Endau River, Holttum 24909; S. Susur Rotan, Holttum 24499. *Selangor*: Telok Reserve, Burkill 6612 (the sterile fronds only; the fertile frond is *Stenochlaena palustris*).

7. **Teratophyllum Koordersii** Holttum *sp. nov.* Pl. 11 and figs. 48, 49.

Pinnae steriles inferiores frondium plantae adultae brevipetiolulatae (petiolulae 3 mm. longae) c. 11 cm. longae et 1.8 cm. latae, basi superiori late cuneatae vel subtruncatae, inferiori anguste cuneatae, textura subcoriaceae, in sicco rubrae; frondes fertiles ignotae; pinnae bathyphyllorum ad 2.5 cm. longae et 1 cm. latae, margine crenulatae, basi valde inequales.

Bathyphylls. Largest fronds 10 cm. long by 4 cm. wide, with about 6 pairs of pinnae, all articulate, the highest largest; largest pinnae 2.5 cm. long by 9 mm. wide, the edges crenulate, the base unequal as in the pinnae of adult fronds, the apex rounded; the lowest pinnae borne close to the rhizome and deflexed across it. Rachis winged throughout, or sometimes only in the upper part. Fibrillose scales, like those on the adult plant, occur on rhizome, rachis, and pinnae. The smallest fronds show some tendency to a dimidiate condition, one frond measuring 4.5 cm. long having four pinnae on one side and only two on the other; there are no fully dimidiate fronds on the specimens examined.

Adult plant. Rhizome 3 mm. in thickness, not aculeate in the specimens examined. Apex of rhizome and very young fronds covered with fibrillose scales. Stipes to at least 10 cm. long, swollen at the base; leafy part of frond 30 cm. long by 17 cm. wide; pinnae on stalks 3 mm. long, about 9 pairs, the largest 11 cm. long by 1.8 cm. wide, the upper base broadly cuneate or in the lowest pinnae subtruncate, the lower base quite narrowly cuneate, widest one third from base and narrowing evenly to the acute apex; the edge entire, often crenulate towards the apex; texture subcoriaceous; the veins fine and prominent on both surfaces (more so below), about 1.5 to 2 mm. apart near midrib, usually forked once or twice, having thickened ends within the leaf margin; the midrib below, and the rachis,



48 and 49, *Teratophyllum Koordersii*, bathyphylls, x ⅔.

bearing numerous fibrillose scales of the type usual in the genus, but larger than those of *T. aculeatum*. Whole plant somewhat reddish when dried. The upper pinnae are often nearly equally cuneate at the base.

TYPE: Celebes, Provincia Minahassa, Koorders 17065B (adult fronds), 17123B and 17064B (bathyphylls). All in the Buitenzorg Herbarium.

The adult and juvenile fronds are on separate sheets, with separate numbers; but two numbers are in sequence, and the similarity in the form of the pinnae, in the scaliness, and in the red colour of the fronds, are evidence that all belong to one species. The bathyphylls are very similar to those of *T. ludens*, but the bases of the pinnae are much more unequal; the adult leaves of the two species are quite distinct. The adult leaves of *T. Koordersii* are perhaps nearest to those of *T. Williamsii*, but the pinnae of the former are thicker in texture, the apex less narrowly acuminate, the base more broadly truncate on the upper side, and the stalks much shorter. The youngest stage, and the fertile fronds, are still required to complete our knowledge of this species.

8. **Teratophyllum arthropteroides** (Christ) Holttum *comb. nov.* Pl. 12.

Stenochlaena arthropteroides Christ, Bull. Boiss. Ser. II, 6, 998 (1906). *Original description.* Rhizomate longe excurrente funiforme pennae gallinaceae crassitie, haud aculeato sed ruguloso, brunneo et squamis furfuraceis atratis adpressis sparso, radicibus more Hederae abunde praedito flexuoso. Foliis sparsis, stipite fulvo stramineo basi articulata, foliorum juniorum brevi, adultorum 5 cm. longo, fronde 25 cm. longo 13 cm. lata ovata, basi vix attenuata, pinnis 8—10 utrinque, patentibus, petiolulatis, callo manifesto nigro racheos insidentibus, rachi tenui, minime alata, fulvo-straminea, squamulis atratis furfuraceis cum nervis facieque inferiori pinnarum sparsa; pinnis plantae junioris 6 cm. longis 18 mm. latis ovato-acutis basi valde inaequalibus, antice auriculato-truncata, postice cuneata, eleganter crenato-serratis; pinnis plantae adultae 9 cm. longis 2 cm. latis lanceolatis, obsolete crenulatis, nervis ultra 1 mm. remotis tenuissimis aut basi aut medio furcatis. Textura tenui herbacea, colora laete virente. Fronde fertili (immatura) pinnis basi ovatis fere cordatis linearibus acuminatis valde remotis. *Hab.* Rio Ampalit, IV, 06. (a specimen of Loher's from the Philippines.)

In 1907, in dealing with the Stenochlaenas of the Philippines, Christ published a further note about this species as follows: " This species is distinguished by its very unequal and crenulate pinnae, one specimen with secondary leaves bearing also many adult leaves, which, although small, are strongly crenulate. The secondary leaves are rather large, 10 cm. long, 4 cm. wide, nearly sessile, tripinnatifid, the rachis reddish, flexuous, the pinnae ovate, obtuse, 2 cm. long, 1 cm. wide, the pinnules serrate, cut into linear segments which are obtuse, often bi-or trifurcate, 2 mm. long, 0.5 to 1 mm. wide, the colour very dark green." It thus appears that the bathyphylls of this species are less finely dissected than those of *T. Williamsii.* I have seen no specimens bearing them, except possibly one (Prov. Bataan, Luzon, Curran, Forestry Bureau no. 19152, in H.C.)

On the specimens I have examined are fronds of varying size, from 14 to 40 cm. long, and pinnae from 5 by 1.5 cm. to 9 by 2 cm. All agree in having stalked pinnae of thin texture with very unequal base (except that the lower pinnae often have the base almost equally cuneate) and veins rather widely separated, and all except the largest fronds have strongly crenulate edges to the pinnae. Elmer's no. 18353 has fronds 40 cm. long, the pinnae almost entire on the Buitenzorg sheet but crenulate on the sheet in Copeland's herbarium, pinna stalks up to 4 mm. long, and a shorter fertile frond with pinnae up to 5.4 cm. long by 7 mm. wide. One of Copeland's specimens from Mt. Maquiling has a complete fertile frond 21 cm. long (including the stipe) and 9 cm. wide, the pinnae to 4.5 cm. by 7 mm.

Specimens seen.

PHILIPPINES. *Luzon*: Rizal Prov., Loher 14809 (HM), 14786 (HM, HCal); Los Banos (Mt. Maquiling), Laguna Prov., Elmer 18353 (HB, HC); Copland s.n. Oct. 1911 (HC). *Mindanao*: San Ramon, 1400 ft., Copeland s.n., Mar. 1905 (HC).

DISCUSSION.

1. *Stenochlaena.*

The distinctions between this and the other two genera are: spores without perispore, pinnae with glands at the base, venation with narrow subcostal areolae from which the other veins spring, and the vascular anatomy of the rhizome radially symmetrical and exceedingly complex. Two of the species have the margins of the pinnae reflexed as in Pteris. Now all these characters are found in the genus Acrostichum. The spores of *Acrostichum aureum* have no perispore, it has a gland on the upper side of the base of each pinna, it has long narrow subcostal areolae from which the other veins spring, and it has a very complex vascular anatomy of rhizome and petiole. I do not here discuss in detail the anatomy of *Acrostichum aureum* and its possible relation to that of Stenochlaena, partly because I have not at present access to previous literature, and partly because I have no material of *S. laurifolia* and *S. areolaris* for dissection and microscopic examination. The problem is a very complex one, and would need elaborate treatment for satisfactory results to be obtained; from my limited observations I can only suggest that a similarity between the vascular anatomy of the petioles of *Acrostichum aureum* and *Stenochlaena palustris* appears possible. It is an interesting fact that *S. laurifolia*, which has pinnae not articulate (a relatively primitive character not normally shared by the other two species) has the largest stem and the most complex anatomy; further, that this species has the edges of the spinnae reflexed, as in the pteroid ferns and in *Acrostichum praestantissimum* (see Bower, Vol. III p. 58). All these facts taken together are strong evidence in favour of a relationship between Stenochlaena and Acrostichum, and hence point to a pteroid origin for Stenochlaena.

It may be urged that in its subcostal areolae Stenchlaena also closely resembles Blechnum. But in Blechnum the subcostal areolae originate in connection with the sori and only occur in fertile fronds, whereas in Pteris and its allies they occur quite independently of the sori and are found equally in both sterile and fertile fronds. In vascular anatomy also Blechnum is relatively simple and offers no indication of a relationship to the complex structure of Stenochlaena. The indications seem to me therefore to point much more strongly to a relationship of Stenochlaena with the Pteroid stock than with Blechnum. Copeland's suggestion of a relationship to Asplenium was evidently based chiefly on the evidence of dissected bathyphylls, which are not found in Stenochlaena; I shall give evidence that even Teratophyllum, which does have dissected bathyphylls, is not nearly related to Asplenium.

The anatomy of the fertile pinnae of *S. palustris* and *S. laurifolia* is interesting; but comparable vascular arrangements are found in other groups of acrostichoid ferns, and it is evident that such anatomical adaptations are accompaniments of the acrostichoid state and can no more be called in evidence of relationship than can the acrostichoid condition itself, except within a narrow range of allience.

2. *Lomariopsis and Teratophyllum.*

These two genera are evidently closely allied, and must be considered together. In view of Christ's reiterated opinion that the bathyphylls of Teratophyllum indicate an origin from Asplenium, I have examined carefully a series of specimens of *A. epiphyticum* Copel. collected near Los Banos by Dr. G. A. C. Herklots. I have also examined all the specimens of this species in the Manila Herbarium. *A. epiphyticum*, when mature, has simple leaves on a slender climbing rhizome. Young plants have bipinnate bathyphylls similar to those of *Teratophyllum Williamsii,* but even more lax in their branching. There are transition leaves showing a long subentire terminal pinna with lateral dissected pinnae below it. In successively higher leaves these lateral pinnae gradually disappear. This is a mode of development quite different from that found in either Teratophyllum or Lomariopsis. When a detailed examination of form and structure is made, *A. epiphyticum* is found to be quite distinct also in other respects from those two genera.

The bathyphylls of *A. epiphyticum* differ from those of Teratophyllum (1) in their much more lax habit, (2) in having pinnae not articulated, (3) in their scales (on veins beneath) which have the lateral walls of their cells much thickened and the superficial walls (and contents) colourless, a type of scale not found in either Teratophyllum or Lomariopsis. The bathyphylls of *A. epiphyticum* agree with those of Teratophyllum in having their lowest segments reflexed to cover the rhizome.

The rhizome of the mature plant of *A. epiphyticum* is quite different in appearance from a Teratophyllum rhizome. It is not dorsiventral; roots and leaves appear on all sides of it. A series of transverse sections shows this very clearly. Such sections (fig. 29—30) show a ring of several vascular bundles, with leaf gaps between them; the bundles on either side of a gap each give off a small branch for the leaf trace, and apparently also any bundle may give rise to a root. The stipe contains only two bundles (as usual in Asplenium). This is quite a different vascular arrangement from that of all species of Teratophyllum and Lomariopsis, which have dorsiventral rhizomes, rooting on one side only, and a ring of several separate bundles in the stipe. All the Asplenium species I have examined possess a radially symmetrical rhizome anatomy similar to that of *A. epiphyticum.*

From the above comparison, particularly as regards the rhizome, I conclude that Teratophyllum and Lomariopsis present important differences from Asplenium, and that we must look elsewhere to find nearer allies. The strong common characters of the two genera are the dorsiventral rhizome and the vascular anatomy of rhizome and stipes. These characters are remarkably uniform within each genus; the two differ constantly in that Teratophyllum has only two rows of leaves on the dorsal side of the rhizome and Lomariopsis several rows. The two differ more markedly in their mode of development and form of leaves. They agree in having similar spores. In searching for their nearest allies, it appears to me that one must look first for ferns with creeping rhizome of similar anatomy and similar anatomy of stipes, and secondly for such as combine such vascular anatomy with comparable leaf form and similar spores. In Campium we have such a group of ferns (limiting that genus as in Christensen 1931, pp. 290—291). The species of Campium have creeping rhizomes with dorsiventral structure and vascular anatomy of both stipe and rhizome essentially similar to those features in Lomariopsis and Teratophyllum, and among them are types of leaf development comparable with both Lomariopsis and Teratophyllum; their spores also are closely similar to the spores of Lomariopsis and Teratophyllum.

The development character of Lomariopsis is as follows; first simple fronds, larger and larger up to a limit, beyond which lateral pinnae appear below the large simple lamina, later fronds having successively more and more lateral pinnae, all of which are articulate while the persistent apical lamina is not. The development of Teratophyllum differs from the very beginning: first come lobed fronds, the lowest lobes early separating as distinct articulate pinnae, successively more and more lobes being cut off from the apical region of the fronds, which apical region never resembles a simple pinna (this condition is seen in the normal bathyphylls); and finally, if my hypothesis is correct, the apex of the frond disappears; thus the pinnae of the adult frond are descended directly from the lateral lobes of the early leaves and are not additions below a matured large apical lamina as in Lomariopsis. *Campium subsimplex* (Fée) Copel. is almost identical with Lomariopsis in its development, the only difference being that the lateral pinnae are not articulate. *Campium quoyanum* (Gaud.) Copel. on the other hand has no definite terminal pinna, and from an early stage its fronds have distinct lateral lobes, more and more of which become separate pnnae. Admittedly the distinction between these two species is not so striking as that between Lomariopsis and Teratophyllum; but it seems to me reasonable to suggest that Lomariopsis and Teratophyllum represent extreme specialised conditions of the two types of development, which coexist, less sharply distinguished, in the less specialised genus Campium. The above similarities, added to the fact that Campium has already developed the acrostichoid condition, are good evidence for the hypothesis that Lomariopsis and Teratophyllum have been derived from Campium, or from the same stock as Campium.

Christensen is of opinion that the species of Campium are acrostichoid derivatives of the Dryopterideae. It is interesting to note that both the types of leaf development above described are found in Dryopteris and also in Aspidium; *A. polymorphum* Wall. and *D. cuspidata* (Wall.) Chr.

represent the one type, *A. malayense* Chr. and most species of Dryopteris the other. The dorsiventral rhizome of Campium must have come as a distinct change from the radially symmetrical rhizomes usual in Dryopteris and Aspidium. The rhizome of even such a long-creeping species as *Dryopteris unita* (L.) O. Ktze has a perfectly radial vascular arrangement, and its leaves and roots are produced on all sides; indeed, among Malayan species of Dryopteris and Aspidium I have not met with any possessing a creeping rhizome of the definite dorsiventral structure found in Campium, Lomariopsis and Teratophyllum. But the stipes of Aspidium and Dryopteris have an open ring of several separate vascular bundles, as also do the stipes of Campium; this is an important point of resemblance of all of them to Lomariopsis and Teratophyllum, and one in which all these genera differ from Asplenium and Blechnum.

I suggest then that Lomariopsis and Teratophyllum have arisen, independently, from Campium, or from the same stock as Campium, both becoming specialised in having high-climbing rhizomes and articulate pinnae, but differing in that Teratophyllum possesses only two rows of leaves and Lomariopsis several rows, and differing also more specially in their mode of development; I suggest that this latter difference goes back to their separate origins at different points in the Campium stock. Teratophyllum is more specialised than Lomariopsis in various points. It has retained in a specialised and persistent form an early developmental stage of its leaves, bearing these special leaves in the lowest stratum of the forest; they may also serve the plant by superficial absorption of water. Its adult leaves have all the pinnae articulate, the apex being possibly aborted. The fertile pinnae are much reduced in width (except in *T. rotundifoliatum*), and have a peculiar vascular system adjusted to their form. The fact of the pecularity of *T. rotundifoliatum* is a definite indication that the form of the fertile pinnae is one of the most easily variable characters, and of much less importance in judging broad questions of relationship than rhizome characters; the venation of fertile pinnae goes hand in hand with their form and is equally subject to variation even between closely allied species. We have seen examples of this also in Stenochlaena.

There are other ferns which seem to me to be also allied to Campium; these are the genus Lomagramma, *Polybotrya Wilkesiana* Brack. and *P. articulata* J. Sm. (the last named I have not seen) and *Lomariopsis Balansae* Fourn. Lomagramma species have rhizomes and stipes which to the eye are hardly distinguishable from those of Lomariopsis, and they have exactly the same internal structure; their scales however are different, having thickened lateral walls to the cells and clear lumina so as to produce a latticed effect, the edge being ciliate much as in Lomariopsis. The fronds of young plants of the lowland species of Lomagramma in the Malay Peninsula are very strikingly similar to fronds of Egenolfia (which is very closely allied to Campium). Their pinnae are articulate (this is probably connected with the high-climbing habit as in Lomariopsis) and have a reticulate venation of a peculiar kind, without free veinlets. It appears to me likely that Lomagramma has been derived directly from a free-veined ancestor, not through one with anastomosing veins, and I suggest that it originated from, or is of common origin with, Egenolfia. The spores of all species of Lomagramma which I have examined have very thin walls, and no perispore, whereas the spores of Egenolfia have a perispore similar to those of Campium. This spore question is one that similar further investigation. I have at present little material of Lomagramma, and find that it rarely produces fertile fronds. *L. perakensis*, which is common in some parts of the Main Range of the Peninsula, grows in small deep shady mountain valleys, starting life on the rocks beside the little streams in the valley bottoms and gradually finding its way to neighbouring tall trees up which it can climb. Recently, after long search, I found sporelings of this species. It is possible that the thin walled spores are related to the peculiarly moist and shady conditions in which this plant always produces its prothallia.

Polybotrya Wilkesiana is different from Lomagramma in many respects, and though Copeland included it in Lomagramma he remarked that perhaps it should form a separate genus, with *P. articulata*; with this opinion I agree, and would include with them *Lomariopsis Balansae*, though I have not yet seen its bathyphylls. *P. Wilkesiana* has adult sterile fronds which are quite indistinguishable from those of Teratophyllum, having free veins and all the pinnae articulated. Moreover, it has bathyphylls which grow to a very large size (30 cm. or more in length), and are bipinnate with the pinnules articulate. Its rhizome is slender like that of Teratophyllum, but has additional bundles in it. I suggest that it is most probable that *P. Wilkesiana* has arisen from Teratophyllum; but it presents such points of difference that it should be placed in a separate genus. I have not at present adequate material to characterise the genus definitely.

SUMMARY.

1. The term bathyphyll is proposed for leaves of a distinctive character borne by a plant in the lowest stratum of the forest.

2. A historical survey is given of the treatment of the genera Stenochlaena, Lomariopsis and Teratophyllum in botanical literature. The three genera have been confused because of a similarity of climbing habit and adult leaf form (both sterile and fertile), and because some collectors have associated the bathyphylls of species of Teratophyllum with adult leaves of species of Lomariopsis and Stenochlaena.

3. The species of the three genera within the Malayan region and the Pacific are described, including two new species and two new varieties.

4. *Teratophyllum luzonicum* and *T. Koordersii* are described as new species; *T. aculeatum* var. *montanum* and *Lomariopsis Kingii* var. *petiolulata* as new varieties. The following new combinations are made: *Lomariopsis intermedia, L. Raciborskii, L. Kingii, L. subtrifoliata, L. Setchellii; Teratophyllum gracile, T. Williamsii, T. rotundifoliatum, T. ludens, T. arthropteroides.*

A full account of all stages of development of *Teratophyllum ludens* and *T. rotundifoliatum* is given for the first time.

5. Teratophyllum alone produces bathyphylls; these are borne not only by young plants but also by branches from the bases of old plants. The distinctive characters of the bathyphylls of the various species are established. Biological notes are given concerning the species native in the Malay Peninsula, particularly as regards early development and the way in which the bathyphylls are borne.

6. A comparative account is given of the morphological, anatomical and developmental characters of the three genera. The genus Stenochlaena differs markedly from the other two genera in its spores, anatomy and venation. These differences are considered to indicate a quite distinct origin for this genus. The genera Lomariopsis and Teratophyllum agree closely together on many points, but differ very constantly in early developmental stages and in the articulation of the terminal pinnae; a separation of the genera is made on these grounds.

7. It is suggested that Stenochlaena originated from the Pteroid stock and points of relationship with *Acrostichum aureum* are noted.

8. Christ's suggestion of a close relationship between Teratophyllum and species of Asplenium which produce dissected bathyphylls is discussed. An account of the developmental history and anatomy of *Asplenium epiphyticum* is given, and important differences between this species and

Teratophyllum are pointed out. It is concluded that Teratophyllum is not nearly related to Asplenium, the supposed relationship resting only on a superficial resemblance of bathyphylls.

9. The differences of developmental history between Lomariopsis and Teratophyllum are discussed, and it is suggested that both are of common origin with Campium, which has similar spores and anatomical characters and in which both forms of developmental history occur. It is further suggested that Lomagramma is an allied genus, possibly originating from Egenolfia, and that the three species *Lomariopsis Balansae* Fourn., *Polybotrya Wilkesiana* Brack. and *P. articulatum* J. Sm. probably constitute a distinct genus, derived from Teratophyllum.

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